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Further studies on the culture of the prawn, *Palaemon serratus* Pennant, with emphasis on the post-larval stages

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Abstract

Following the work of Reeve (1969) the conditions for optimum growth and survival of juvenile prawns was studied. After metamorphosis the young prawns were weaned from the larval diet of live *Artemia* nauplii to prepared foods such as the flesh of mussels, crabs, shrimps and lugworms. This change was sometimes associated with high mortalities, which could be reduced if a mixture of live and prepared foods was supplied during the first few days. Mussel was the best and most commonly used of the four prepared foods, but there was some evidence to suggest that a combination of two prepared foods was better than each food fed singly. After weaning, these foods proved satisfactory in long-term experiments and several prawns were reared to maturity, spawned and gave rise to healthy larvae.

Cannibalism of the newly-moulted prawns was the major cause of mortality in the laboratory and was positively correlated with the population density. The level of cannibalism was dependent on the area of tank floor per prawn rather than the volume of water available. The presence of horizontal shelves in the tanks reduced cannibalism by 40 per cent in one experiment.

The optimum temperature for growth was 20–24°C; above 24°C mortality increased. Prawns were found to be tolerant of a wide variety of water conditions, provided that the oxygen level was maintained.

In a large-scale rearing experiment 18 500 (36.1 per cent) post-larvae were obtained from 51 300 larvae distributed between six 75-litre polythene rearing bins. Some of these were subsequently reared outdoors during the summer under a variety of conditions in twelve wooden tanks measuring 4 feet × 4 feet × 11 inches (approx. 1.2 × 1.2 × 0.3 m) (water depth 6 inches, approx. 15 cm). Each tank was stocked with 500 post-larvae. In 138 days from June to October an average of 56.9 per cent survived and reached a mean live-weight of 1.29 g. The various conditions tested made little difference to survival or growth.

It is concluded that although it would be biologically possible to culture *P. serratus* on a commercial scale, it is unlikely to be an economic success. Work on the rearing of other species of prawn is recommended.

Further studies on the culture of the prawn, *Palaemon serratus* Pennant, with emphasis on the post-larval stages

Introduction

A programme designed to study the possibility of culturing the prawn, *Palaemon serratus* (Pennant), in the United Kingdom was started at Conway by Reeve in 1964. He showed (Reeve 1969) that it was possible to culture larvae which had been hatched from egg-carrying females and that juvenile prawns resulting from successful larval development would survive and grow well in the laboratory.

Ling and Merican (1962) showed that another palaemonid prawn, *Macrobrachium rosenbergii* (de Man), can also be cultured in the laboratory, and Ling (1967a) outlined a method for rearing and culturing one million juveniles. In Japan Hudinaga (1942), Hudinaga and Miyamura (1962), Hudinaga and Kittaka (1967) have cultured the shrimp, *Penaeus japonicus* Bate, and have successfully developed the rearing technique to a commercial scale.

The objectives of the work reported in the present paper were to study the conditions necessary for successful growth and survival of prawns at all stages of their post-larval life, and if possible to obtain an estimate of how long it would take juveniles grown in such conditions to reach a commercially acceptable size.

The work was done at the Shellfish Culture Unit, Ministry of Agriculture, Fisheries and Food, Fisheries Experiment Station, Conway, where the laboratory has been specially designed for the study of culture requirements of marine shellfish (Walne 1966).

Experiments with Mature Prawns Captured from the Wild

Initially experiments were made using mature wild prawns which had been captured in traps or by hand netting. Results of experiments using such animals were however unsatisfactory, since in the laboratory they showed a high rate of mortality and no growth. The following example is typical of the results obtained with a wild stock. Thirty-five prawns with an average total length of 8.0 cm, and an average live-weight of 3.2 g, were kept in each of three 50-litre tanks with a constant flow of sea water. One tank was maintained at each of three temperatures, 10, 15 and 20 ± 1°C. A weighed quantity of mussel (*Mytilus edulis*) was added daily as food and any which remained after 24 hours was removed, thoroughly blotted with tissue paper, and weighed. After 5 weeks, during which an average of 0.11 g mussel per prawn per day was consumed, the surviving prawns were counted and weighed. A second count was made after 8 weeks but the prawns were not weighed. The results were as follows:

Temperature (°C)	Number of prawns after		Average weight of prawns (g)	
	5 weeks	8 weeks	Initially	After 5 weeks
10	19	15	3.22	3.18
15	29	3	3.12	3.01
20	20	3	3.26	3.00

Other experiments using a similar procedure but varying the food, the flow of water and the number of prawns in each tank were equally unsatisfactory, since they also showed high mortalities and little or no growth (see Table 1). In many of the experiments a decrease in weight was recorded. During these experiments the prawns continued their moulting cycle, since exuviae were frequently found in the tanks. From a tank containing 35 prawns, as many as 4 exuviae were found on some days. In spite of this there was no growth in the tank populations. Reeve (1969) also found that mature wild-caught prawns kept individually in 1-litre beakers failed to increase in weight during a period in which they each moulted three times. The failure of mature prawns to grow in the laboratory is not understood. It is thought that the diet was adequate since juveniles subsequently captured from the wild and fed only with mussel grew well.

The inability of mature wild-caught prawns to adapt to laboratory conditions was also reflected in the high mortalities observed in these initial experiments. Although cannibalism of the newly-moulted prawns was responsible for up to 50 per cent of the mortalities in some experiments, other mortalities occurred frequently, the cause of which was not so obvious. Such mortalities were uncommon in laboratory-reared juveniles and in juveniles captured from the wild. Reeve (1969) reports the occurrence of two diseases from which prawns will die—*brown spot*, where the cuticle becomes covered in small brown spots, and *white tail* or *white spot*, where the posterior part of the abdomen becomes an opaque dull white. The opacity spreads quickly through the rest of the abdomen, within 24–48 hours depending on temperature, resulting in death within the next 24 hours. It was noticed during this work that *white tail* was often associated with either the disappearance of a posterior abdominal appendage and the subsequent decay of the cuticle at the site of the wound, or erosion of the cuticle at the anal opening.

Brown spot has not been observed in laboratory populations since December 1965. *White tail* has recurred, however, particularly in mature prawns captured from the wild during the winter months of 1965 and 1966. It was responsible on one occasion for the loss after only 6 weeks of 1 000 mature prawns which were kept outside in wooden trays. At this time the temperature of the water in the trays ranged

between 4.5 and 8°C. *White tail* has been observed only occasionally in laboratory populations of juveniles and has only once been responsible for significant mortalities in such populations. Its cause is not known, but it seems to be associated with low temperatures and erosion of the cuticle on the abdomen.

There was also a significant proportion of mortalities among mature prawns which had no obvious cause. Reeve (1969) reports such mortalities as occurring just prior to moulting. However, mortalities also occurred during the moult itself when the prawns seemed to be incapable of freeing themselves from their exuvia. In this condition they died within 24 hours, if they were not first attacked by other prawns in the tank. Mortalities of this kind during the moult have also been seen among laboratory-reared juveniles.

Attempts to improve tank conditions and thus prevent high mortalities among mature prawns were unsuccessful. The flow of water through the tanks was varied, and antibiotics and chlorine (1 p.p.m.) were added to the water in an unsuccessful attempt to combat *white tail.* Dipping prawns in stronger solutions of chlorine, 3 and 5 p.p.m., also failed. Different kinds of cover had no effect in protecting newly-moulted prawns from cannibalism (Reeve 1969). Later observations on stock prawns showed that a mixed diet of crab (*Carcinus maenas*) cut into halves, crushed shrimp (*Crangon vulgaris*) and mussel also failed to improve survival.

It was concluded that adult, wild-caught prawns were unsuitable for laboratory studies. Adult prawns are now used for breeding purposes only, and since attempts to induce females to spawn in the laboratory have met with only spasmodic success, the laboratory breeding stock is limited to those females which are carrying eggs.

Table 1 Percentage survival and percentage change in live-weight of wild-caught mature prawns kept under different conditions for 5 weeks

Experimental treatment	Number of prawns	% survival after 5 weeks	% weight change after 5 weeks
Population density varied; no shelter in tanks	20	65	−1.5
	45	47	−0.4
	65	38	−7.8
	85	34	+6.6
Population density varied; shelter in tanks	20	60	+7.0
	45	51	−5.3
	65	52	+7.6
	85	36	−1.4
Food: fresh mussel	35	54	−7.3
boiled mussel	35	54	−7.9
fresh mussel + liver + fish meat	35	69	−5.1
Static filtered water changed three times per week	35	49	−1.9
Flowing water	35	57	−8.3

Methods

Experimental animals All the experiments described below were made with young prawns (juveniles) which ranged in size from 6 mg (8 mm total length) immediately after metamorphosis to about 2 g (males) and 3.5 g (females), at which sizes the sexes reach maturity. Juveniles were obtained using the mass rearing technique described on pages 27–36. Hatchery-reared juveniles were used in most experiments, although young wild-caught prawns were used during the autumn months when it was not possible to rear a supply of juveniles in the laboratory. These adapted well to laboratory conditions and showed good survival and growth in several experiments.

Experimental vessels These included 1-litre glass beakers, 8-litre polythene buckets, 12-litre polystyrene aquaria, 25- and 50-litre white polythene tanks, 75-litre black polythene dustbins, 140-litre grey fibreglass tanks and 280-litre white fibreglass tanks.

Seawater supply Most experiments were made using static water which was always kept well aerated and was changed twice per week. Experimental tanks were placed in water baths and maintained at $20 \pm 2°C$.

Food supply and preparation The foods provided were mussels (*Mytilus edulis*), crab (*Carcinus maenas*) and shrimp (*Crangon vulgaris*). Lugworms (*Arenicola marina*) were used occasionally when they were available and *Artemia salina*, both nauplii and adults, were given to juveniles immediately after metamorphosis. The value of these foods is discussed below. In experiments not concerned with food requirements a combination of two and sometimes three foods was used. Mussels and shrimps were used most commonly since they fragmented less easily than crab, and therefore did not foul the water as quickly; lugworms were not readily obtainable in large numbers. The prawns were fed every day and any food left from the previous day was removed.

The foods were prepared in the following ways. Mussels were opened into halves and the meat left on the shell, except in small-scale experiments where pieces of meat were fed. Crabs were cut into halves longitudinally, shrimps were either cut into small pieces or crushed, and lugworms were chopped into several pieces. These foods will subsequently be called prepared foods.

All the foods were collected locally. Crabs and mussels were gathered in large numbers and kept alive in outdoor storage tanks until they were required. Initially shrimps and lugworms were stored in this way until it was found that they could be satisfactorily deep-frozen. Tests showed that juvenile prawns grew and survived equally well on both fresh and deep-frozen shrimp and lugworm.

Weighing of live animals In many experiments an estimate of growth rate was required. This was estimated in terms of increase in live-weight per unit time. The method of live-weighing which was used gave consistent results and caused no apparent harm to the prawns.

Early juveniles were live-weighed in batches of up to 500. They were removed from their tanks with a fine-mesh strainer and placed on several layers of tissue paper so that much of the water clinging to their exoskeletons was absorbed. They were then brushed into a dry container and weighed, after which they were returned to their tanks. Later juveniles were not weighed in this way because they jumped off flat sheets of tissue paper. Instead they were put into a cylinder which contained strips of tissue. The cylinder and prawns and tissue strips were shaken gently for 10 seconds. The juveniles were separated from the tissue paper and put into a dry container to be weighed. As many as 150 juveniles could be conveniently weighed together in this way.

It was realized that these methods of removing excess water were not entirely efficient. However, consistent results were obtained from repeated weighings of the same populations over a 24-hour period if they were dried for a standard length of time with plenty of tissue paper. An example of the variation which occurred in such test weighing is as follows:

Weighing	Recorded live-weight of 25 juveniles (g)	Percentage deviation from mean
1	35.057	0.014
2	35.300	0.679
3	35.035	0.077
4	34.972	0.257
5	35.106	0.125
6	34.900	0.464

It is seen that in these six weighings the deviation from the mean did not exceed 0.7 per cent. The above procedure for live-weighing juveniles was therefore adopted and used throughout the course of this work.

Measurement of total length In some experiments it was desirable to measure the length and length increments of prawns. The total length from the tip of the rostrum to the distal end of the telson was the measurement used. Early juveniles, from 8 to 20 mm in length, were measured to the nearest 0.1 mm below, under a binocular microscope fitted with a graduated eyepiece, and prawns from 20 mm upwards were measured to the nearest mm below, with a ruler.

Food Requirements and Growth Rates

THE FOOD REQUIREMENTS OF JUVENILES AFTER METAMORPHOSIS

Some early experiments indicated that there was a critical period immediately following metamorphosis when heavy mortalities occurred. It was thought that these mortalities may have been due to changing the food from *Artemia* nauplii to various prepared foods. The severity of the critical period and the influence of the different diets was shown in the following experiment, in which 150 newly-metamorphosed juveniles were added to each of six 50-litre tanks at $20 \pm 2°C$. Different foods were supplied to each tank: fresh mussel, boiled mussel, pieces of female crab gonad and digestive gland, chopped shrimp, pieces of fresh, white-fish muscle and *Artemia* nauplii. After 6 days the juveniles remaining in each tank were counted, as follows:

Food	Survivors	Food	Survivors
Fresh mussel	67	Shrimp	94
Boiled mussel	93	Fish	89
Crab	121	*Artemia* nauplii	128

These results suggested that live food may improve survival immediately following metamorphosis, although the juveniles fed with female crab gonad and digestive gland also did quite well.

Observations showed that late larvae and early juveniles readily ate 6 to 10 day-old *Artemia* (termed

grown *Artemia*) which had been fed on the unicellular algae *Isochrysis galbana* and *Tetraselmis suecica*. It was also observed that pieces of female crab gonad and digestive gland were taken by early juveniles in preference to the other prepared foods, e.g. mussel and shrimp. Accordingly an experiment was made to test the effect of *Artemia*, crab and combinations of these two foods on the survival and growth of newly-metamorphosed juveniles. Twenty weighed juveniles were added to a duplicate series of five 1-litre beakers at 20 ± 2°C. *Artemia* nauplii, grown *Artemia*, pieces of female crab gonad and digestive gland, *Artemia* nauplii + crab, and grown *Artemia* + crab were supplied to the different beakers. In the beakers to which *Artemia* + crab was added, the amount of crab was gradually increased and the supply of *Artemia* reduced so that after 7 days only crab was provided. The juveniles were therefore gradually weaned on to prepared food. After 11 days the juveniles were counted and weighed (see Table 2). In this experiment grown *Artemia* had a beneficial effect on both survival and growth, and as a result were generally used as a weaning food together with pieces of crab.

With some batches of juveniles less difficulty was experienced in weaning from live to prepared foods. For example, in one experiment 50 newly-metamorphosed juveniles were kept individually in 1-litre beakers at 20 ± 2°C. They were divided at random into five groups of ten, each group being fed with one of the following: grown *Artemia*, female crab gonad and digestive gland, shrimp, mussel gonad and lugworm. After 14 days only one death had occurred and this was in one of the beakers fed with shrimp where the prawn died during its first post-larval moult. Another experiment was made in which 100 weighed newly-metamorphosed juveniles from a later batch than those in the above experiment were divided equally among four 25-litre tanks at 20 ± 2°C. Two of the tanks were supplied with newly-hatched and grown *Artemia* and two with pieces of female crab gonad and digestive gland. After 14 days the juveniles were counted and weighed:

Food	Number of prawns	Average live-weight (mg)
Artemia	92	23.60
„	86	19.05
Crab	91	16.16
„	94	15.28

There was no difference in survival between crab-fed and *Artemia*-fed juveniles, and the larger weight increase recorded for the *Artemia*-fed animals was not significant ($P > 0.05 < 0.10$). However, this result is similar to that of the feeding experiment described above (see Table 2) and therefore suggests that grown *Artemia* will give better growth than crab gonad and digestive gland among newly-metamorphosed juveniles.

It is not clear why some batches of juveniles and not others could be transferred directly from live to prepared food with little mortality. It was noticed that juveniles reared during the latter part of the research programme showed a less severe critical period. It is possible therefore that the modifications and improvements to the larval rearing technique made throughout the work led to the production of juveniles in a stronger condition which were better able to survive the changes of diet. Another possibility is that there may be differences between juveniles from different stocks. During the course of the work egg-carrying females were obtained from Weymouth (Dorset), Par (Cornwall) and Holyhead (Anglesey); however, no comparative experiments were made to examine possible differences between juveniles from these different sources.

Since good survivals were obtained in later batches of juveniles immediately after metamorphosis when fed with prepared foods, an experiment was made to test the influence of different prepared foods and food combinations on survival and growth. Batches of 20 newly-metamorphosed juveniles were weighed and added to each of a duplicate series of eight 1-litre beakers at 20 ± 2°C. The beakers were supplied

with the following foods: female crab gonad and digestive gland, shrimp, lugworm, mussel gonad, and combinations of two of the above, i.e. crab + lugworm, crab + mussel, shrimp + lugworm and lugworm + mussel. Crab + shrimp and shrimp + mussel were also tested, but high mortalities occurred as a result of air failure. After 11 and 21 days the survivors were counted and weighed. The results given in Table 3 show that there was no significantly improved survival or growth on any of the single food diets, or on any of the combined diets. However, there was a highly significant increase in growth on combined food diets when compared with the single foods ($P < 0.001$). There was no correspondingly improved survival between the juveniles fed on the single and combined foods.

The explanation for the improved growth on combined food diets is unknown. It may be that juveniles will eat more when fed with two foods, or that two foods form a nutritionally more complete diet which gives more rapid growth. Further investigation is needed on this point and also on the effects of feeding three and four foods in combination.

THE FOOD REQUIREMENTS OF LATER JUVENILES

Later juveniles from about 2 weeks after metamorphosis readily ate crab, mussel, lugworm and shrimp. No critical evaluation of these foods fed singly and in combination was made with later juveniles, but two experiments suggested that there was little difference in their food value. The first compared the growth of two groups of 50 juveniles fed on crab and mussel, and kept in two 25-litre tanks which were supplied with a gentle flow of sea water at $20 \pm 2°C$. The second experiment compared the growth of three groups of 85 juveniles from the same stock as those above when fed with crab + mussel, crab + shrimp and mussel + shrimp. These juveniles were kept in 50-litre tanks which were also supplied with a gentle flow of sea water at $20 \pm 2°C$. In both experiments the prawns were counted and weighed weekly over a period of 63 days,

Table 2 The influence of live food on the survival and growth of batches of 20 newly-metamorphosed juvenile prawns, average live-weight 5.57 mg. In the beakers to which both *Artemia* and crab were added the supply of *Artemia* was gradually decreased so that after 7 days only crab was supplied

Food	Number of prawns after 11 days	Average live-weight after 11 days (mg)
Artemia nauplii	10	14.24
,,	12	11.91
Grown *Artemia*	19	16.75
,,	20	20.26
Crab	11	16.75
,,	17	16.46
Artemia nauplii and crab	20	14.44
,,	14	14.44
Grown *Artemia* and crab	20	17.13
,,	19	18.28

Table 3 Growth and survival of batches of 20 newly-metamorphosed juvenile prawns fed with single and double food diets

Food	Number of prawns after		Average live-weight (mg) after		
	11 days	21 days	0 days	11 days	21 days
Crab	11	10	5.37	16.75	36.32
,,	17	11	5.37	16.46	34.61
Shrimp	12	6	5.37	14.77	36.58
,,	13	11	5.85	14.34	37.06
Lugworm	10	10	5.37	14.45	30.81
,,	13	9	5.37	14.32	37.60
Mussel	15	10	5.85	16.70	44.38
,,	11	5	5.85	13.86	31.33
Crab and lugworm	16	12	5.85	17.79	42.87
,,	17	12	5.85	18.59	45.32
Crab and mussel	18	7	6.47	17.81	44.93
,,	11	9	6.47	16.85	43.26
Lugworm and shrimp	10	9	5.85	20.86	54.68
,,	11	9	6.47	17.24	45.58
Lugworm and mussel	12	11	6.47	18.13	41.61
,,	15	10	6.47	16.17	43.63

Table 4 A comparison of the growth of juvenile prawns in two separate experiments in which single and double food diets were provided

Days after beginning of experiment	Average live-weights (g) of juveniles on different diets				
	Mussel	Crab	Crab and mussel	Crab and shrimp	Mussel and shrimp
0	0.095	0.12	0.11	0.13	0.14
7	0.15	0.16	0.17	0.19	0.21
14	0.20	0.21	0.24	0.25	0.29
21	0.26	0.29	0.32	0.34	0.37
28	0.34	0.37	0.38	0.40	0.46
35	0.42	0.45	0.43	0.47	0.53
42	0.49	0.51	0.51	0.54	0.63
49	0.57	0.57	0.58	0.62	0.70
56	0.66	0.64	0.66	0.71	0.77
63	0.74	0.75	0.76	0.81	0.88

and the results are tabulated together in Table 4. The two curves drawn in Figure 1 show the growth on mussel and on mussel+shrimp respectively; similar curves for growth on the other foods, i.e. crab, crab+mussel and crab+shrimp, lie between these two lines. The similarity in growth on the different diets is in contrast to the results obtained for newly-metamorphosed juveniles, when a combination of two foods gave better growth than single foods. Further investigation is, however, needed to confirm these observations and also to test the value of other foods such as fish meat or fish offal, and further combinations of foods to later juveniles.

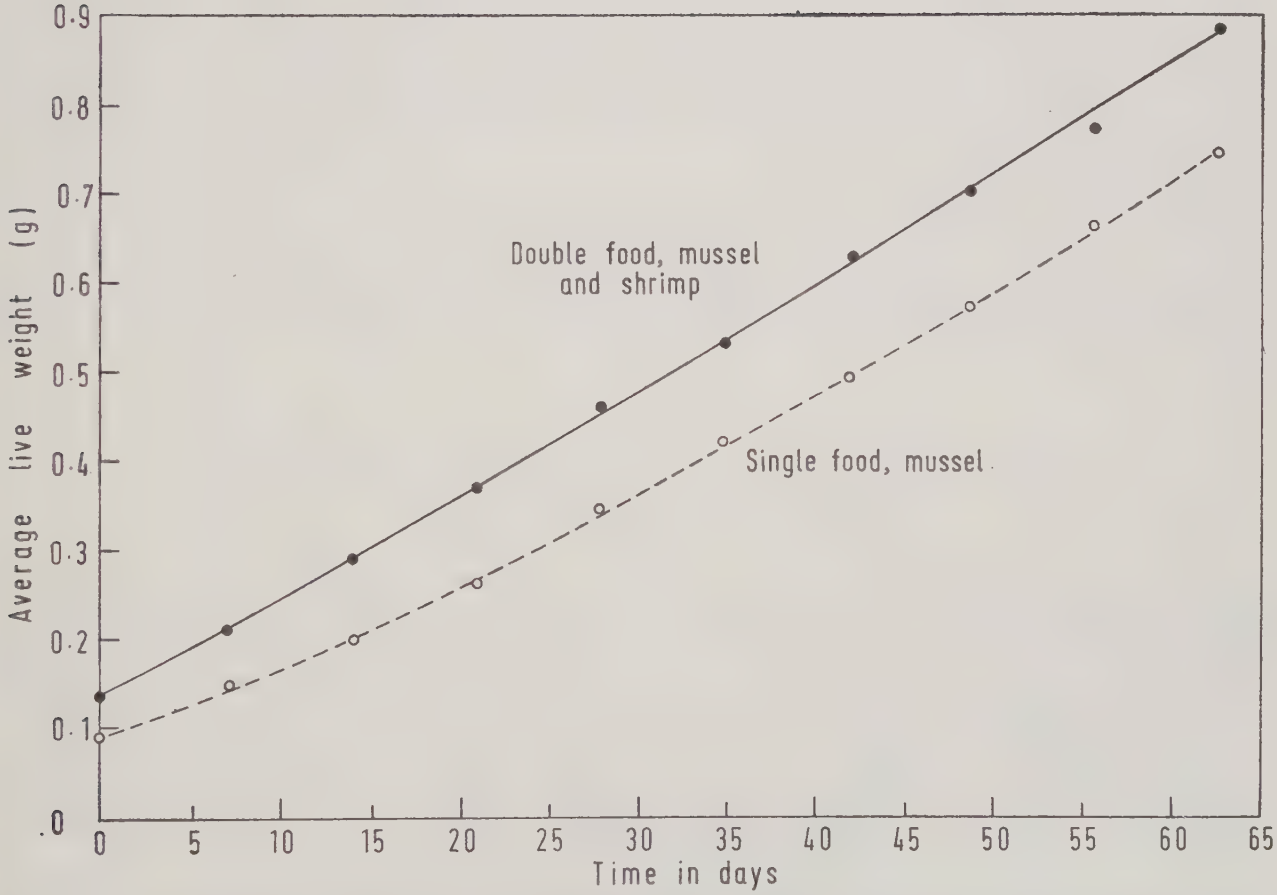

Figure 1 A comparison of the growth of juvenile prawns in two separate experiments in which single and double foods were provided.

Normally for prawns not being used in feeding experiments and for stock prawns a combination of two foods from crab, mussel or shrimp was provided. The adequacy of such diets was shown when the three groups of 85 prawns on combined diets in the above feeding experiment were kept for a further 6 months under the same conditions. They were counted and weighed monthly and the final average live-weights and numbers surviving were as follows:

Food	Number of prawns after 239 days	Average live-weight (g)	
		Initially	After 239 days
Crab and mussel	7	0.11	2.78
Crab and shrimp	8	0.13	2.55
Shrimp and mussel	12	0.14	2.88

There were 27 prawns left in the three tanks at an average live-weight of 2.74 g. Of these 22 were males and 5 were females; the females were noticeably larger than the males and had developed mature ovaries which could be clearly seen through the carapace. All of the females underwent the pre-mating moult and one copulated successfully following the moult and laid viable eggs. Two became victims of cannibalism after the moult and two failed to copulate and laid non-viable eggs; both these females became victims of cannibalism at their next moult. The remaining 22 males were put together in a 140-litre fibre-glass tank provided with a gentle flow of sea water at $20 \pm 2°C$ and fed with a mixture of crab, shrimp and mussel; 19 of these animals were still alive 187 days later at an average live-weight of 3.35 g. Figure 2 shows the growth of all the prawns fed on combined food diets for 426 days. The last part of this curve from 2.74 to 3.35 g (239 to 426 days) represents the growth of males only, which at 3.35 g are approaching their maximum size. Females, however, will grow to 10 g in their natural environment and it is possible that in a mixed population the last part of the growth curve may be steeper than is shown in Figure 2. The exact shape of the curve during this part of the life cycle remains to be determined. However, females generally mature at 3.0 to 3.5 g live-weight and much of their growth effort following maturity is directed to the maturation of their ovaries. It is expected, therefore, that although the growth curve for a mixed population may be steeper than is shown in Figure 2, the growth rate will slow down at the 3.0 to 3.5 g stage.

FEEDING EXPERIMENTS WITH JUVENILES KEPT INDIVIDUALLY

A more detailed investigation of the influence on growth of different single foods was made by studying the moulting frequency and increase in total length per moult of juvenile prawns kept individually in 1-litre beakers at $20 \pm 2°C$. Ten prawns were fed for 11 weeks on each of the following: grown *Artemia*, crab gonad and digestive gland, shrimp, lugworm, and mussel gonad. The beakers were inspected each morning for exuviae which could be seen at the bottom of the beaker when a prawn had moulted, and any prawn which had moulted within the previous 24 hours was measured. After moulting some prawns consumed their own exuviae and some moults almost certainly went unrecorded as a result. Such an error could be recognized, however, by an uncharacteristic gap in the moulting pattern of the prawn concerned and also by an unusually large increase in length between the recorded moults.

In Table 5 the mean lengths after 24 and 70 days are given. These means do not include the lengths of all the prawns which were alive after these intervals, because some measurements were missing due to unrecorded moults. The results show that there are small differences in the values of these foods to prawns. Analysis of variance of the results after 24 days shows significant differences between the foods (variance

ratio = 5.50; $P < 0.01$) and that mussel is superior to the other foods, with grown *Artemia* second. The standard errors and calculated 99 per cent confidence limits of the mean lengths are given in Table 5. Analysis of variance of the results after 70 days shows a less significant difference between the foods (variance ratio = 3.47; $P < 0.05 > 0.01$), which is partly due to there being fewer measurements and partly to a greater variability. The standard errors and 95 per cent confidence limits of the mean lengths are given in Table 5. Mussel continued to give the best growth, although there was some overlap at the 5 per cent level with grown *Artemia*, shrimp and crab. Lugworm gave the poorest growth.

It had been observed previously that grown *Artemia* gave better growth than crab gonad (see Table 2), but the improved growth on mussel was not expected, particularly since early juveniles ate crab in preference to mussel when both were offered. The superiority of mussel was confirmed in another experiment when three batches of eight individually-kept newly-metamorphosed juveniles were fed with mussel, crab and shrimp respectively for 21 days:

Food	Mean length (mm)	Standard error	99 per cent confidence limits
Mussel	18.96	0.278	18.24–19.68
Crab	16.10	0.278	15.38–16.82
Shrimp	15.81	0.278	15.09–16.53

Plankemann (1935) suggested that a mussel diet, which is rich in glycogen, may influence the moulting frequency of *Leander squilla* (*Palaemon elegans*) and *Crangon crangon*. The observed differences in growth on the various foods in the above experiment could therefore be associated with differences in the moulting

Table 5 The results of an experiment in which five batches of 10 newly-metamorphosed juvenile prawns were kept individually in 1-litre glass beakers and fed with different foods

Food	After 24 days				After 70 days			
	Mean length (mm)	Number of prawns measured	Standard error	99% confidence limits	Mean length (mm)	Number of prawns measured	Standard error	95% confidence limits
Grown *Artemia*	18.01	8	0.204	17.48–18.54	39.56	8	1.303	37.01–42.11
Crab	15.99	9	0.181	15.52–16.46	38.42	6	1.504	35.47–41.37
Shrimp	16.79	8	0.204	16.26–17.32	38.43	7	1.392	35.70–41.16
Lugworm	16.67	6	0.272	15.97–17.37	35.13	8	1.303	32.58–37.68
Mussel	19.83	7	0.233	19.23–20.43	42.29	7	1.392	39.56–45.02

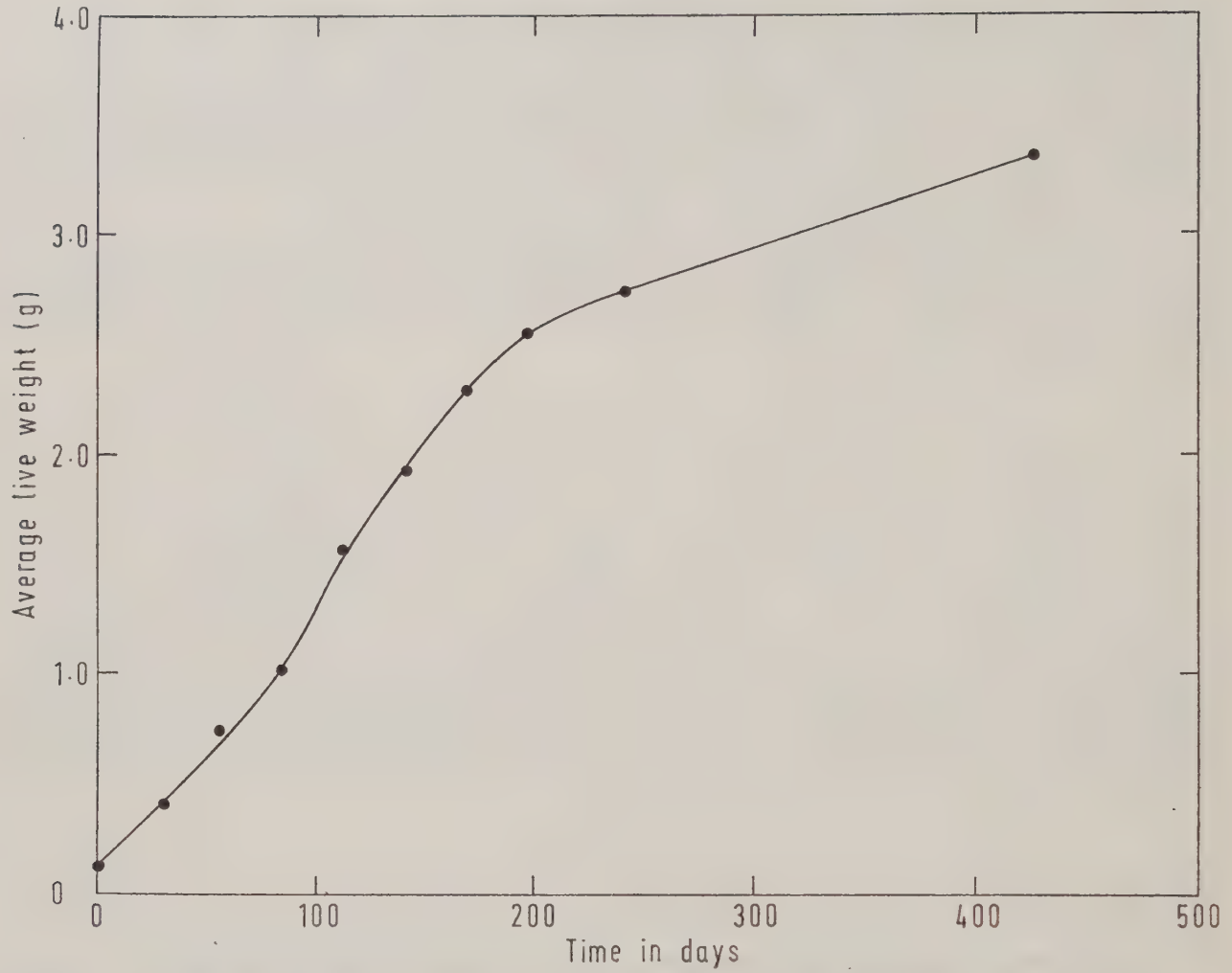

Figure 2 Growth of a population of laboratory-reared juvenile prawns in 426 days. The increase between days 239 and 426 is the growth of males only, since there were then no females in the population.

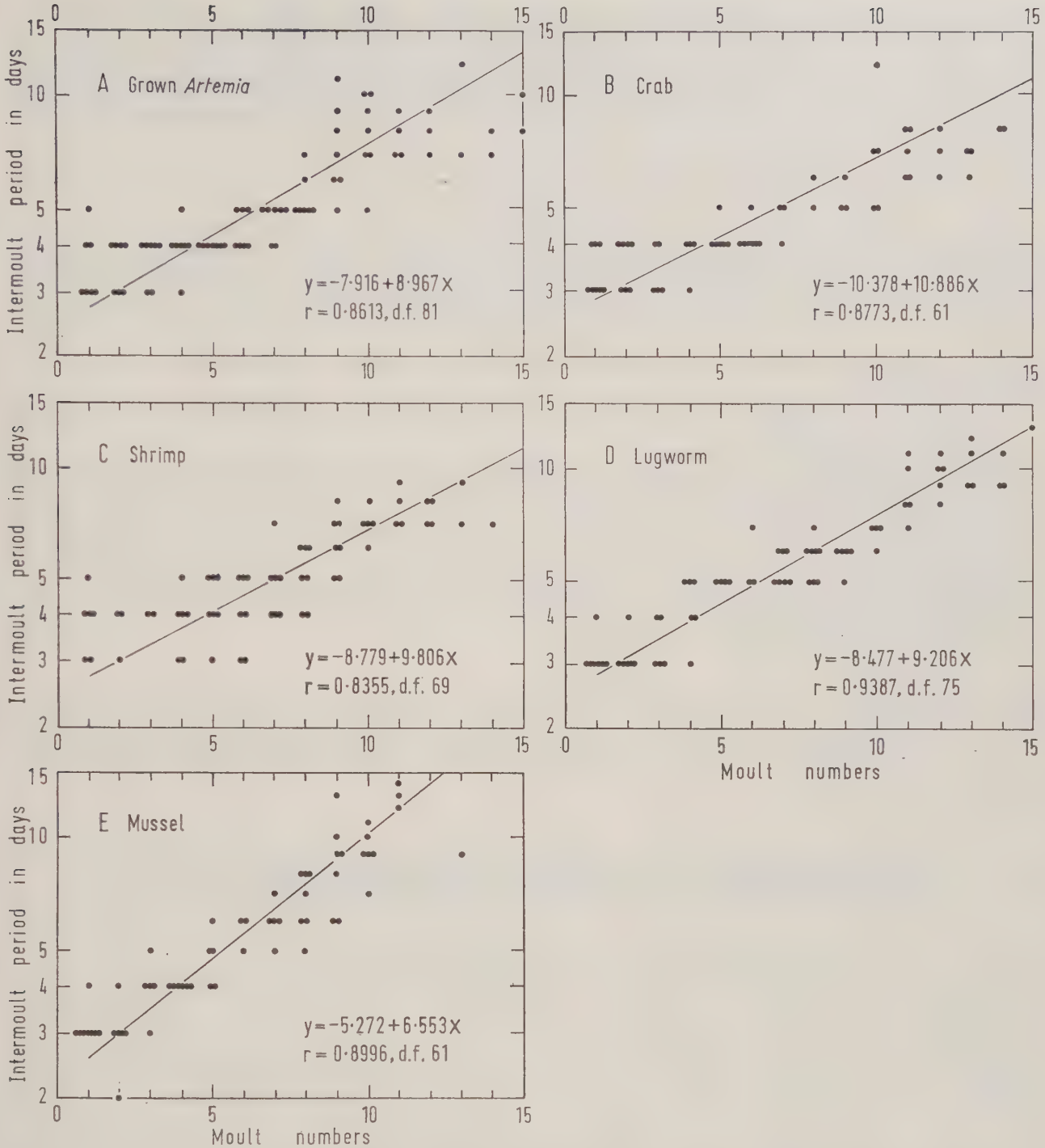

Figure 3 Log_e intermoult period plotted against moult number for prawns fed with various foods. The experiment was made with five batches of ten newly-metamorphosed juveniles kept individually in 1-litre glass beakers. The calculated regression lines are drawn.

frequency. The moulting patterns of the prawns fed on different diets were shown by plotting $\log_e$ intermoult period in days against the moult number (Figure 3). The only significant difference was between mussel- and crab-fed prawns (t: 2.357; $p < 0.02 > 0.01$), showing that crab-fed prawns moulted more frequently than those on mussel. The faster growth observed on mussel and grown *Artemia* cannot therefore be explained by a higher moulting frequency and was due to a greater increment at each moult (see Table 6).

GROWTH TYPE

Hiatt (1948) introduced a method of describing crustacean growth by plotting pre-moult length against post-moult length. Kurata (1962) used this method when postulating three growth types for crustacea which depend on the value of the growth coefficient. He defines the growth coefficient as b in the equation:

$$L_{n+1} = a + bL_n,$$

where L_n = pre-moult length, L_{n+1} = post-moult length, and a = constant. The three types of growth described by Kurata are:

1. progressive geometric growth, where successive post-moult increments increase with the increase of pre-moult size, i.e. $b > 1.0$;
2. retrogressive geometric growth, where successive post-moult increments decrease with the increase of pre-moult size, i.e. $b < 1.0$;
3. arithmetic growth, where successive post-moult increments are independent of pre-moult size and remain constant, i.e. $b = 1.0$.

For practical purposes Kurata adopted the following criteria for distinguishing growth types:

1. progressive geometric growth $b \geqslant 1.05$;
2. retrogressive geometric growth $b < 0.95$;
3. arithmetic growth $b < 1.05 \geqslant 0.95$.

Kurata showed that in many crustacea there are changes in the growth type associated with different stages in the life cycle. Larval life is frequently characterized by arithmetic growth, and following metamorphosis there is a change to progressive geometric growth; at maturity another change, to retrogressive geometric growth, occurs.

Table 6 The average length increment per moult of five batches of 10 newly-metamorphosed juvenile prawns kept individually in 1-litre beakers and fed with different foods

Food	Average length increment (mm) at moult number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Grown *Artemia*	0.94	1.05	1.40	1.90	2.21	2.29	2.76	3.43	3.49	3.31	3.21	3.71	2.65
Crab	0.36	0.99	1.29	1.46	1.48	2.00	1.50	1.65	3.00	1.90	3.13	4.25	3.38
Shrimp	0.71	0.70	0.75	1.80	2.45	1.50	1.99	2.90	3.39	3.94	3.58	2.88	3.50
Lugworm	0.36	0.68	0.83	1.17	1.63	1.98	2.08	2.38	2.24	3.13	3.88	3.40	3.00
Mussel	0.55	1.13	1.34	1.66	2.31	2.37	2.93	2.74	3.08	4.00	3.50	3.70	4.75

The data obtained from the individual feeding experiment described above were graphed according to the method of Hiatt. The regression equations are given in Table 7 and the curve for mussel is drawn in Figure 4; the other foods gave similar curves. Also given in Table 7 are the calculated standard errors and 95 per cent confidence limits of b. These data show that although there were differences in the growth rate on the different diets the growth type of all the juveniles was the same, i.e. progressive geometric.

A Hiatt diagram was also constructed using the length increments recorded from 12 prawn larvae kept individually in 1-litre beakers at $20 \pm 2°C$ and fed with *Artemia* nauplii (see Figure 5), and the regression data were as follows: $y = 0.9604x + 1.1464$; $r = 0.9705$; d.f. $= 48$; s.e. of $b = 0.03443$; 95 per cent confidence limits of $b = 0.893—1.028$. These data show that larval growth may be either retrogressive geometric or arithmetic and therefore that there is a change in growth type to progressive geometric at metamorphosis. Further measurements on larval growth are needed to distinguish precisely the growth type at this period. Measurements on the growth of older prawns at maturity were not made.

FOOD CONVERSION EFFICIENCY

One experiment was made in order to obtain an estimate of gross conversion efficiency, expressed as increase in live-weight/wet weight of food eaten $\times 100$, in young prawns. Fifty small juveniles were added to each of three 50-litre tanks at $20 \pm 2°C$, and fed with weighed halves of shrimp for 9 weeks. Shrimp was chosen as the food because after 24 hours in sea water it stayed firm and the remaining food could therefore be easily retrieved and weighed. Food was provided only just in excess, in order to reduce inaccuracies due to the loss of weight of shrimp meat left in water for 24 hours. The halves of shrimp were thoroughly blotted with tissue before weighing and the prawns were weighed weekly according to the procedure outlined earlier.

Table 7 Hiatt growth data, where y = post-moult length L_{n+1} and x = pre-moult length L_n, for five batches of 10 newly-metamorphosed juvenile prawns kept individually in 1-litre glass beakers and fed with different foods

Food	Regression equation	Correlation coefficient	Degrees of freedom	Standard error of b	95% confidence limits of b
Grown *Artemia*	$y = 1.0810x + 0.8287$	0.9937	77	0.01392	1.054–1.108
Crab	$y = 1.1368x - 0.2877$	0.9971	63	0.01091	1.116–1.158
Shrimp	$y = 1.1302x - 0.0894$	0.9962	56	0.01321	1.104–1.156
Lugworm	$y = 1.1160x - 0.1118$	0.9961	87	0.01061	1.095–1.137
Mussel	$y = 1.1261x - 0.0150$	0.9979	63	0.00921	1.108–1.144

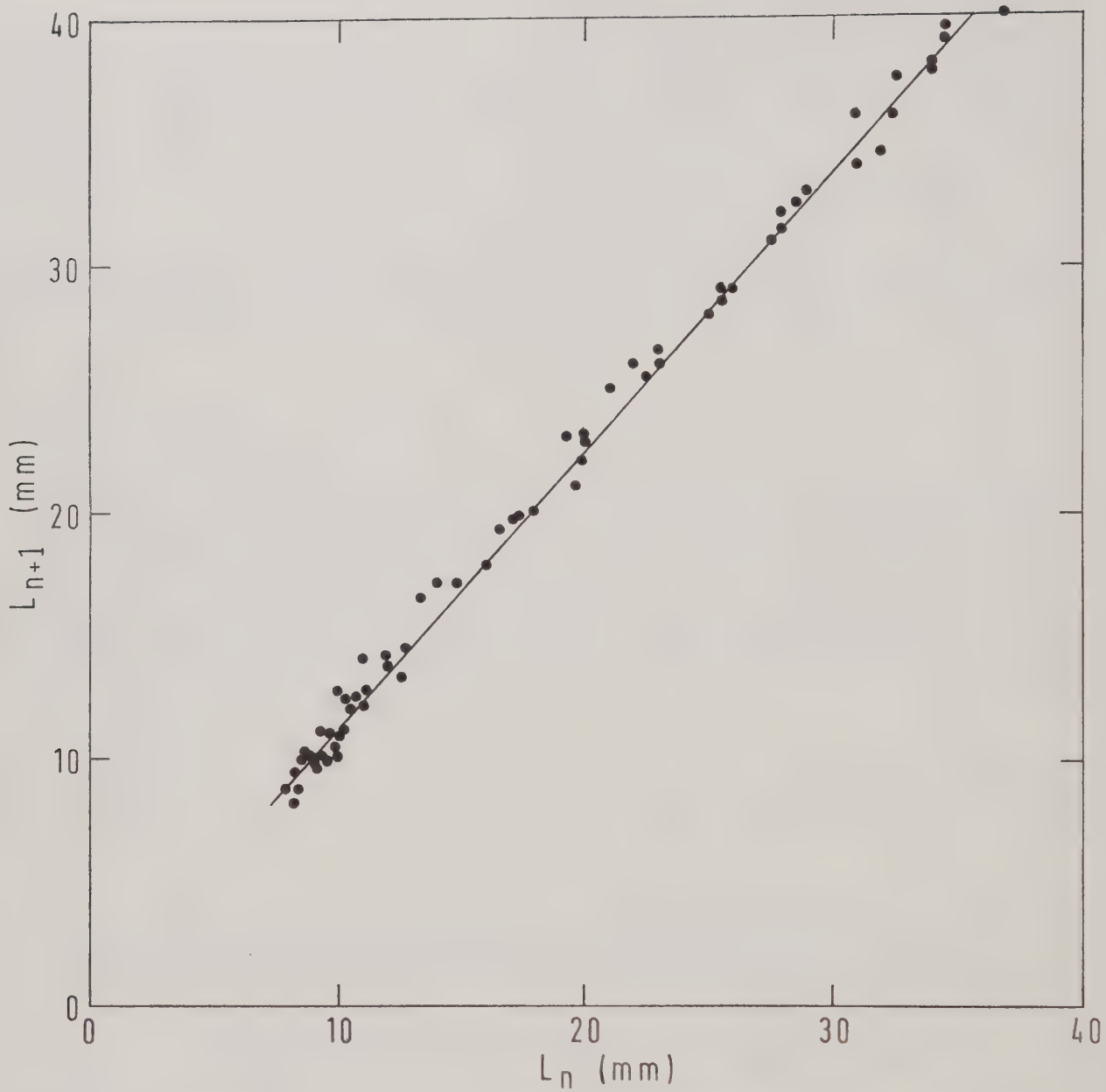

Figure 4 A Hiatt diagram for ten newly-metamorphosed juvenile prawns kept individually in 1-litre beakers and fed with mussel. The calculated regression line is drawn.

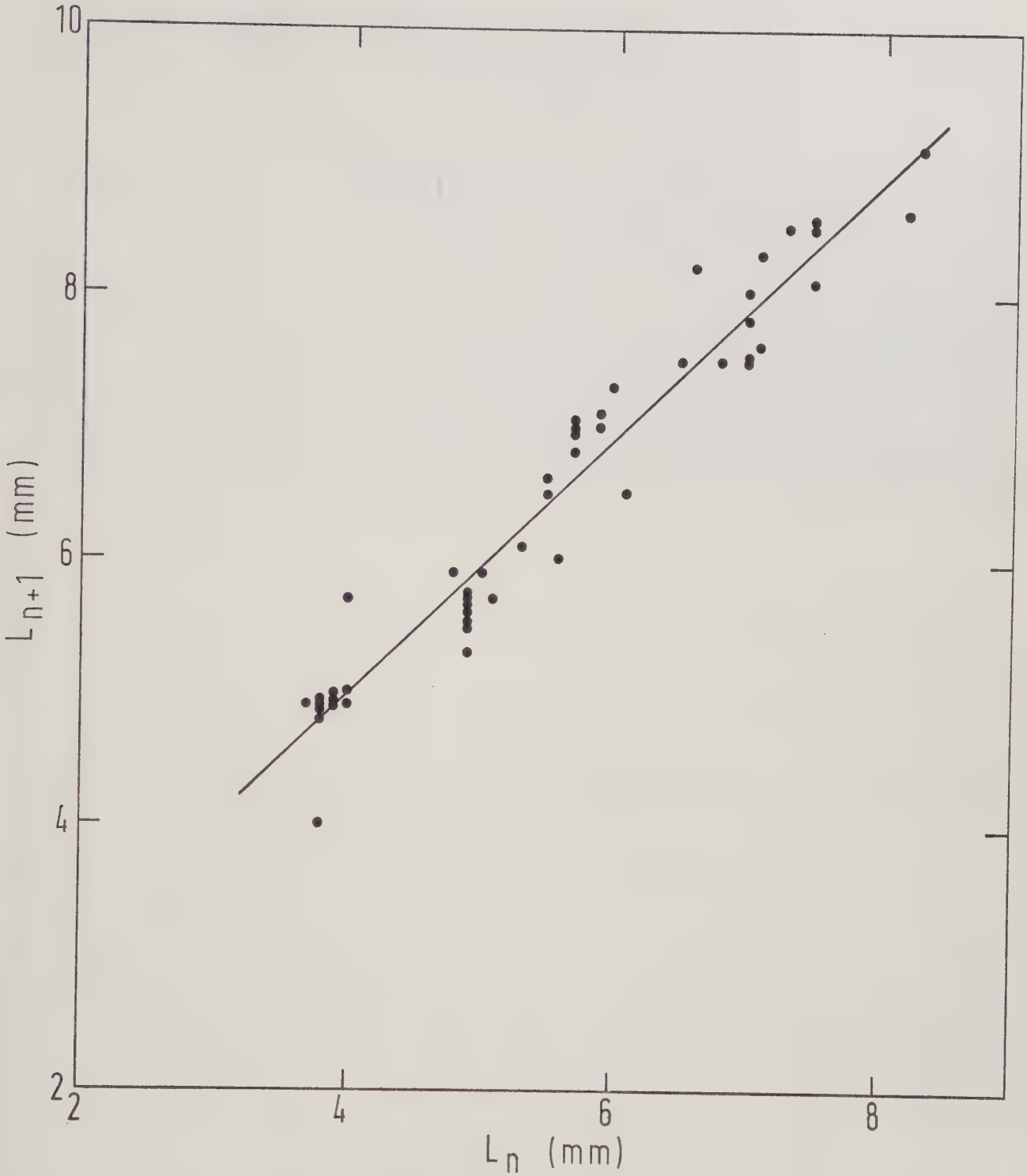

Figure 5 A Hiatt diagram for twelve prawn larvae kept individually in 1-litre beakers and fed with *Artemia* nauplii. The calculated regression line is drawn.

The mean food conversion efficiency over 9 weeks (see Table 8) was 18.9 per cent, which represents a considerable reduction from the 35 per cent found by Reeve (1969) for larvae feeding on *Artemia* nauplii. If the results are graphed (Figure 6) a straight line relationship is obtained which is highly significant ($P < 0.001$); the regression equations are as follows:

Regression	Regression equation	Correlation coefficient	Degrees of freedom
x on y	$y = -0.5454x + 31.025$	−0.7052	25
y on x	$y = -0.0271x + 24.956$	−0.7052	25

It is probable however that the values recorded in this experiment are part of a gently sloping curve and that a straight line relationship has been obtained only because the conversion efficiency was estimated within a comparatively small size range (36 to 444 mg). According to an extrapolation of the straight line relationship shown in Figure 6 prawns would stop growing before they reach 1 g in weight. While it is appreciated that this experiment did not give an accurate estimate, it does show that the conversion efficiency of young prawns declines quite markedly with increasing size and that larger prawns are unlikely to have a gross conversion efficiency greater than 10 per cent when fed on shrimp.

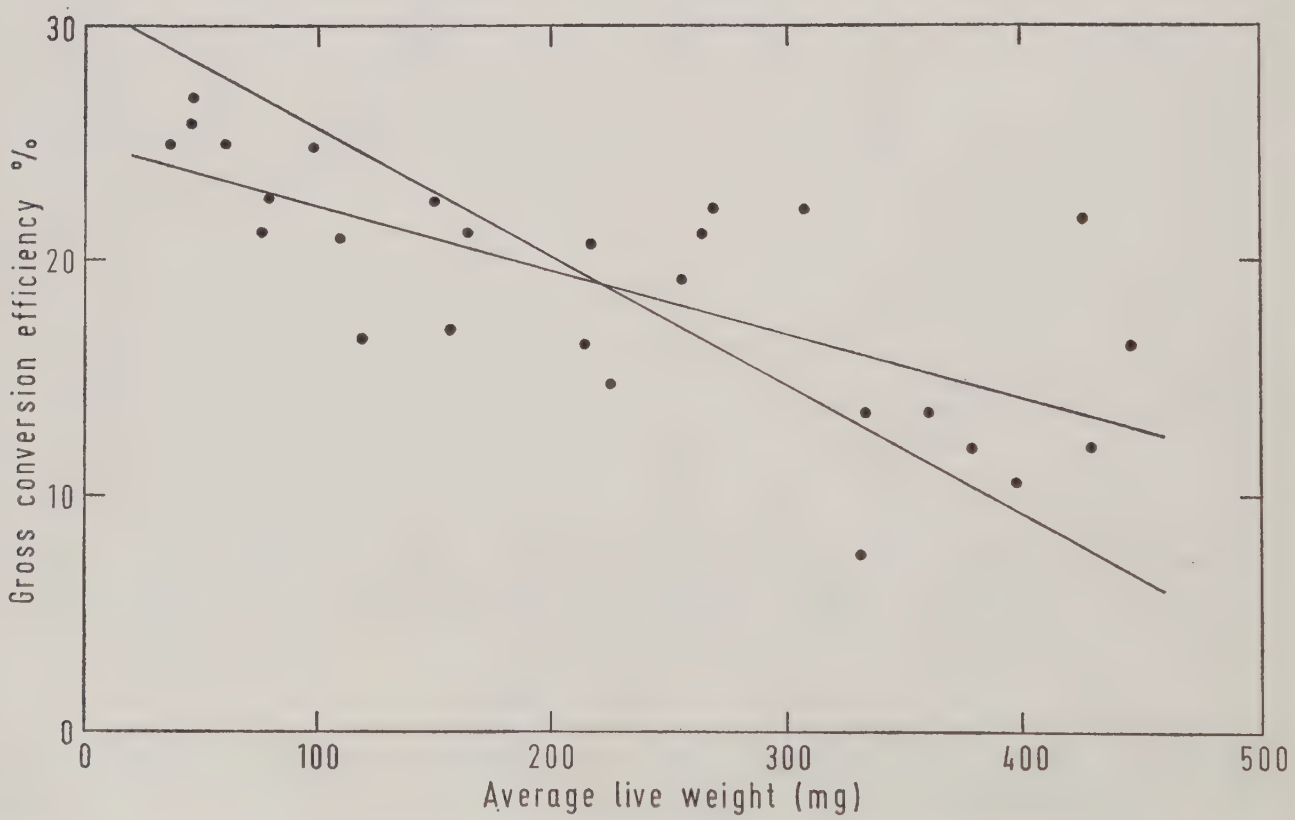

Figure 6 The gross conversion efficiency, plotted against the average live weight, of young prawns fed with shrimp. The regression lines of x on y and y on x are drawn.

Cannibalism and Population Density

BEHAVIOUR OF NEWLY-MOULTED PRAWNS

By far the greatest single cause of mortality in laboratory populations of juveniles was cannibalism. This occurred when freshly-moulted, soft prawns were attacked and eaten by other hard-shelled animals.

Newly-moulted prawns in laboratory tanks rested on the bottom until attacked by other prawns. They then escaped by swimming upwards and remained swimming for about one minute before returning to the bottom where they became subject to further attack. These escape attempts were repeated until either the soft animal was caught or the shell had hardened sufficiently to afford protection. The time taken from moult to a stage when soft prawns are no longer susceptible to cannibalism is not known accurately, but is probably only a few hours. The ultimate fate of newly-moulted prawns in laboratory tanks therefore depends on the length of time for which they can sustain their escape efforts, and how successful they are. Newly-moulted prawns would not hide in lengths of rubber and P.V.C. tubing or holes drilled in masonry, and in the laboratory were never seen to exhibit obvious hiding behaviour.

In the experiments to be described below all recorded mortalities are considered as instances of cannibalism, which is a reasonable assumption since there were only a very few mortalities from other causes. In such cases the hard-shelled corpses were removed from the tank as they occurred; unfortunately, however, these were not recorded.

Table 8 Relationship between average live-weight (mg) at the beginning of each week and the gross conversion efficiency (as increase in live weight/wet weight of food eaten x 100) of young prawns fed with shrimp

Week	Replicates					
	1		2		3	
	Average live-weight	Conversion efficiency	Average live-weight	Conversion efficiency	Average live-weight	Conversion efficiency
1	36.48	24.9	45.22	25.7	45.60	26.8
2	60.52	24.9	74.77	21.1	78.69	22.5
3	97.67	24.7	108.5	20.9	117.5	16.6
4	148.8	22.4	156.4	17.0	162.7	21.1
5	213.4	16.4	216.0	20.6	224.3	14.7
6	267.6	22.1	264.1	21.0	255.2	19.1
7	330.5	7.5	332.6	13.5	307.3	22.1
8	359.8	13.5	397.1	10.5	379.1	12.0
9	428.8	12.0	444.5	16.4	425.1	21.7

CANNIBALISM AND THE AVAILABILITY OF FOOD

Ling and Merican (1962), working on *Macrobrachium rosenbergii*, report that only when prawns are inadequately fed do they become cannibalistic. This was not the case with *P. serratus*, since cannibalism was recorded in many experiments in which a surplus of food was always present. Under these circumstances, however, the victim was often only partly eaten by the removal of the appendages.

SEGREGATION OF THE SEXES AND CANNIBALISM

Ling and Merican (1962) report that there were no observed instances of cannibalism among female *M. rosenbergii*. No such observations had been made in the present work and the belief that cannibalism was not restricted by sex was confirmed by the following experiment. Three 50-litre tanks were stocked respectively with 76 males, 76 females, and 38 of each sex. The mean length was 30 to 40 mm which is the smallest size of prawn that can be readily sexed. After 6 weeks at $20 \pm 2°C$ survival was similar in the three tanks:

Sex ratio		Number of prawns surviving after	
♂	♀	3 weeks	6 weeks
76	0	56	17
0	76	34	19
38	38	46	19

RELATION BETWEEN CANNIBALISM AND POPULATION DENSITY

The influence of population density was studied by stocking a replicate series of four 8-litre buckets with 25, 50, 100 and 200 early juveniles respectively. After 15 days at $20 \pm 2°C$ the numbers of survivors were counted, and the results are given as the mean survival and the calculated instantaneous coefficients of mortality (Z):

Initial number of prawns to each tank N_o	Average number of prawns after 15 days N_t	N_t/N_o	Z_t	Instantaneous coefficient of mortality, Z
25	14.5	0.580	0.544	0.036
50	26.0	0.520	0.653	0.044
100	41.5	0.415	0.879	0.059
200	60.5	0.303	1.194	0.080

Figure 7, curve A, shows the relationship between Z and the number of juveniles per bucket, which is plotted on a logarithmic coordinate. The value of Z is calculated from the equation of Beverton and Holt (1956):

$$N_t = N_o e^{-zt},$$

where N_t = number of prawns surviving after time t, N_o = initial number of prawns, Z = instantaneous coefficient of mortality, and t = time interval between measurements. The results show that mortality, and therefore the frequency of cannibalism, increases in relation to the population density.

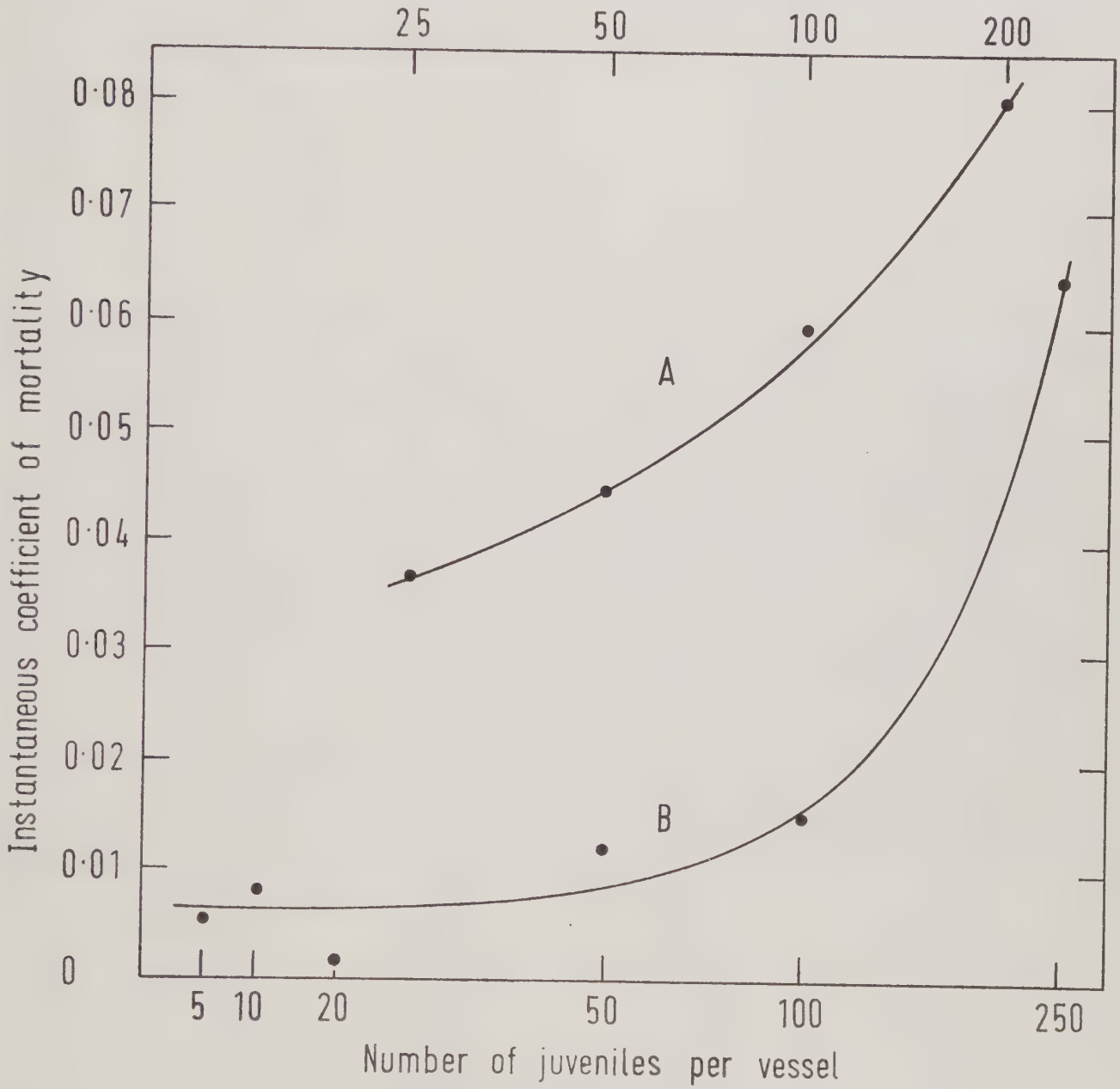

Figure 7 Relation between population density and mortality in juvenile prawns.
A. Newly-metamorphosed juveniles kept for 15 days at 20 ± 2°C in four 8-litre buckets.
B. Older juveniles (30–40 mm total length) kept for 20 days at 20 ± 2°C in six 25-litre tanks supplied with flowing water.

A further experiment was made in which a duplicate series of six 25-litre tanks were stocked respectively with 5, 10, 20, 50, 100 and 250 juveniles between 30 and 40 mm total length. Each tank was supplied with flowing water at 20 ± 2°C. In this experiment the density was held constant over the study period of 20 days by replacing eaten prawns every 2 days from a control stock. The results are as follows:

Number of juveniles per tank N_o	Average daily mortality	N_t	N_t/N_o	Z
5	0.025	4.975	0.9950	0.0050
10	0.075	9.925	0.9925	0.0075
20	0.025	19.975	0.9988	0.0010
50	0.575	49.425	0.9885	0.0115
100	1.450	98.550	0.9855	0.0145
250	15.500	234.500	0.9380	0.0640

The curve (Figure 7B) is steeper than that in Figure 7A; this was expected since the population numbers were held constant by restocking in the later experiment, but they were continually reduced throughout the earlier experiment. The results again show that mortality is directly related to population density.

An experiment run concurrently with the latter test estimated the moulting frequency of individuals from the same stock. Twenty juveniles were kept in 1-litre beakers at 20 ± 2°C. During the study period the average intermoult period was 7.4 days. From this figure an estimate of the number of moults which occurred in the experimental density tanks over the same period can be made. Assuming that all mortalities in the experiment were due to cannibalism (see page 19), the percentage of moulting prawns succumbing to cannibalism can be calculated (Table 9). These figures show that at a density of 250 prawns per 25-litre tank, or 10 per litre, a juvenile has only an even chance of surviving a moult. At a lower density, e.g. one prawn per 2.5 litres, a juvenile has an 18:1 chance of surviving a moult. Although it is realized that the value of 18:1 applies only to the particular size of prawns used in this experiment (viz. 30 to 40 mm), a value of this order represents an unacceptably high level of cannibalism, since it takes many more than 18 moults for prawns to reach a commercially acceptable size.

Table 9 The influence of density on the survival chances of moulting juvenile prawns (30–40 mm) held in 25-litre tanks supplied with a flow of sea water at 20 ± 2°C. The mean values from a duplicated series are given

Number of prawns per tank	Number of moults expected in 20 days	Total mortalities occurring in 20 days	Percentage of moulting prawns cannibalized
5	13.4	0.5	3.7
10	26.8	1.5	5.6
20	53.6	0.5	0.9
50	134.0	11.5	8.6
100	268	28.5	10.6
250	671	309.5	46.1

INFLUENCE OF TANK FLOOR AREA ON CANNIBALISM

Juvenile prawns which are not disturbed usually stay on the bottom of their tanks and are rarely seen clinging to the sides or swimming in midwater. This suggested that in order to control cannibalism the tank floor area available to each prawn was more important than the volume of water.

An experiment was made in which 50 juveniles between 30 and 35 mm mean length were kept at 20 ± 2°C in a duplicate series of three different types of vessel; each contained 9 litres of water but the floor areas were 284, 600 and 2 100 cm². The depths of water were 30, 15 and 4 cm respectively. The mean survivals after 3, 6 and 9 weeks show higher survivals in the two tanks with the larger floor area:

Tank floor area (cm²)	Number of prawns surviving after		
	3 weeks	6 weeks	9 weeks
284	34	15	9
284	35	17	8
600	22	14	11
600	32	16	7
2 100	36	27	22
2 100	42	32	28

Although further replicates of the above experiment were needed to establish the significance of the improved survival it was on the basis of these results that an attempt was made to increase the effective floor area of a deep tank by providing a stack of black P.V.C. sheets mounted horizontally on a wooden frame and spaced about 5 cm apart. The juvenile prawns utilized the extra floor space thus made available by resting on the upper surface of each sheet and by clinging to the underside.

The influence of these *spacers* or artificial floors on the frequency of cannibalism was tested in four 25-litre tanks; two controls had no spacers provided, and two had stacks of three P.V.C. sheets. Each tank contained 150 juveniles (45 to 55 mm total length). Counts were made every 2 days and eaten prawns were replaced to keep the population density constant. The numbers of deaths after 18 days were 143 and 187 in the two control tanks and 79 and 118 in the tanks with spacers. Although mortalities were high—due to the high density of prawns—they were lower, 3.65 per cent per day, in the tanks with spacers, compared with 5.93 per cent per day in the controls.

The experiments reported later in this paper suggest that cannibalism may be further reduced by growing prawns in large tanks while maintaining a relatively high density. Prawns kept in large tanks tend to cluster along the sides and in the corners. This behaviour leaves large unpopulated areas in the middle of the tanks where newly-moulted prawns can remain undisturbed while their new shells harden.

The Influence of the Physical Environment

TEMPERATURE

The influence of temperature on the survival and growth of juvenile prawns was investigated in the range 18–26°C since it was expected that the optimum temperature would fall between these limits. Reeve (1969) showed that the optimum temperature for larval development lay between 22 and 26°C.

Three experiments were made with three different batches of juveniles of different initial average live-weights kept at five temperatures, 18, 20, 22, 24 and 26 ± 1°C. Batches of 50 juveniles of average weight 8.6 mg and 20 of 84.6 mg were kept in 12-litre polystyrene aquaria standing in water baths, and batches of 20 juveniles weighing on average 271.7 mg were kept in 25-litre tanks, also in water baths. The prawns were counted and weighed after 2 weeks and again after 4 weeks at the end of the experiment. The fortnightly increase in average live-weight at each temperature, expressed as a percentage of the increase at 20°C, was calculated for each temperature. The results are given in Table 10, together with the percentage survival after 4 weeks. Although there was considerable variation the results suggest that the optimum temperature for both survival and growth is between 20 and 24°C. At 18°C growth was generally retarded although survival was good, and at 26°C although growth was good, survival was poor.

These results have important implications if the rearing of *P. serratus* is to be attempted as a commercial proposition, for in this country it is only during late June, July, August and early September that temperatures reach 20°C outdoors in static water tanks and ponds. At other times of the year artificial heating would be required if the growth rate was to be maintained at the maximum. Further work on the growth at lower temperatures within the range 6–18°C is required, so that the cost of maintaining elevated temperatures artificially throughout the rest of the year can be compared with the estimated delay in growth if heat is not provided.

LIGHT INTENSITY

The influence of light intensity on growth and survival was studied. Fifty newly-metamorphosed juveniles were added to each of eight 12-litre clear polystyrene aquaria standing on a white background. The aquaria were arranged so that two were in total darkness, two were exposed to a natural diurnal cycle, and the other four were subjected to continuous illumination from a tungsten filament bulb at either 6 or 100 lumens per square foot at the water surface. The aquaria exposed to natural light were shielded from direct sunlight and the light intensity at the water surface varied between total darkness at night to 100 lumens per square foot on bright days. The water temperature in the aquaria under continuous illumination fluctuated between 24 and 26°C and could not be conveniently lowered; the aquaria in natural light and total darkness were therefore maintained at 25°C in a water bath.

The experiment was continued for 6 weeks, the prawns being counted and weighed every two weeks. The results are given in Table 11, which shows the fortnightly average live-weights and the final percentage survival after 6 weeks. Two of the aquaria were discontinued following heavy mortalities due to air failure. In both of the natural daylight aquaria small losses occurred also due to air failure, but there were enough survivors for these to be continued; however, the low final survivals recorded in these aquaria are not meaningful.

The results show that the growth of juveniles was substantially improved in total darkness by comparison with the other light conditions, but survival was reduced. There appears to be no advantage conferred by continuous illumination at the intensities tested in this experiment, but it is possible that continuous illumination below 6 lumens per square foot may result in improved growth.

Table 10 The influence of temperature on the growth and survival of three sizes of juvenile prawns. The fortnightly weight increments are expressed as a percentage of the increment at 20°C

Initial average live-weight (mg)	Temperature (°C)	Weight increase in 2 weeks as a percentage of increase at 20°C		Percentage survival after 4 weeks
		1st fortnight	2nd fortnight	
8.6	18	82.8	54.5	94
	20	100.0	100.0	86
	22	90.8	124.0	80
	24	109.2	114.6	72
	26	78.6	123.0	48
84.6	18	67.9	84.9	95
	20	100.0	100.0	95
	22	113.0	75.3	90
	24	120.7	95.4	95
	26	127.9	57.3	80
271.7	18	87.4	99.7	95
	20	100.0	100.0	100
	22	88.6	103.1	95
	24	89.8	140.3	95
	26	130.1	86.8	60

Table 11 The influence of different lighting conditions on the growth and survival of batches of 50 juvenile prawns, initial average live-weight 8.30 mg

Lighting conditions	Average live-weight (mg) after			Percentage survival after 6 weeks
	2 weeks	4 weeks	6 weeks	
Total darkness	47.4	153	461	46
	43.1	164	–* discontinued	–
Natural daylight	51.0	130*	287	48
	45.5	125*	267	40
Dim light, 6 lm/ft²	40.4	121	250	60
	43.7	135	270	56
Bright light, 100 lm/ft²	46.0	132	249	68
	38.4	–* discontinued	–	–

*Mortalities occurred due to air failure.

Reeve (1969) found that larvae kept in total darkness survived less well than those under natural lighting conditions, and that animals kept in darkness were almost colourless compared with the richly pigmented control animals. This was not the case with the juveniles in the last experiment. Although survival was not as good in total darkness these prawns were much more highly pigmented than those under natural lighting conditions. This suggests that at metamorphosis there may be a fundamental change in the mechanism controlling the chromatophores.

SALINITY

Reeve (1969) suggests that in larvae there may be a small positive correlation between growth and salinity within the range 23 to 32.5‰. The work of Pannikar (1940) showed that *P. serratus* had a fairly wide tolerance to a variety of salinities, particularly in the low range, and would survive at salinities as low as 10‰. The ability to withstand low salinities was more pronounced in young prawns than in adults. The tolerance of young prawns to low salinities was seen in the present work in the experiments described below, when juveniles kept in static water out of doors survived well although on occasion, particularly after heavy rain, the salinity dropped as low as 20‰.

WATER CONDITION

Initially all experimental and stock tanks were provided with a constant flow of heated sea water. Such a system, however, was inconvenient when many small aquaria were used in experiments and also expensive, since large quantities of heated sea water were required. Accordingly, tests were made to establish whether a continuous flow of water was essential to survival.

An experiment was set up in which 80 juvenile prawns were added to each of six 50-litre tanks at 20 ± 2°C. The tanks were arranged so that two had flowing water, two had standing water which was changed twice a week, and two had standing water changed once a week. The average percentage survivals after 33 days were 41, 51, 45 per cent respectively; growth was not recorded. In the tanks which were only changed weekly the water became so turbid during the course of a week that neither the prawns nor their food could be seen at the bottom of the tank. In order that the prawns could always be observed in their tanks it became standard procedure in later experiments to change the water twice per week. Further experiments have confirmed that prawns are very tolerant of turbid water conditions with considerable bacterial proliferation, provided that the dissolved oxygen level is maintained by vigorous aeration.

Reeve (1969) reports that prawn larvae survive slightly better in ultra-violet irradiated filtered sea water than in untreated water. A comparison between the survival of 100 early juveniles in treated and untreated sea water showed that no advantage was conferred by such treatment:

Seawater treatment	Percentage survival after 3 weeks
Unfiltered, not irradiated	35
,,	45
Filtered, ultra-violet irradiated	28
,,	20

Large-Scale Rearing

During the spring and summer of 1967 the small-scale laboratory experiments were expanded into a larger-scale rearing technique. This can be divided into three phases: (1) large-scale rearing of the larvae, (2) laboratory weaning of newly-metamorphosed juveniles, and finally (3) outdoor rearing of juveniles. These three phases are described below.

LARGE-SCALE LARVAL REARING

Previous attempts had been made to provide stocks of juveniles for laboratory studies by rearing batches of 50,000 larvae in each of three 280-litre white fibreglass tanks. They were provided with a constant flow of heated sea water at $20 \pm 2°C$ and were fed with *Artemia salina* nauplii. The overall survival to metamorphosis was only 3 per cent, which was poor compared with an average survival of 35 to 45 per cent quoted by Reeve (1969) in small-scale larval rearing experiments. This poor survival was probably due to two factors: (i) an insufficient supply of food, and (ii) over-vigorous aeration, which was used to disperse the larvae which tended to accumulate in the most highly illuminated areas of the tanks. Reeve (1969) has shown that larval survival is adversely affected by too vigorous aeration.

In April 1967 another attempt was made to rear large numbers of larvae, using 75-litre black polythene dustbins as the rearing vessels. The problem of larval aggregation was thus partially overcome, because all the illumination was from overhead. The bins were supplied with a constant flow of sea water at $20 \pm 2°C$ at about 0.5 litres per minute. The water overflowed from each bin through a filter of 124μ nylon mesh which retained both the larvae and the *Artemia* nauplii provided as food. The filter was cleaned every day, since it readily became clogged with detritus and *Artemia* egg cases which were unavoidably added with the nauplii. A constant flow of water through the bins eliminated the need for complete water changes and the larvae were therefore disturbed as little as possible. Detritus which collected at the bottom of the bins was siphoned off once a week through a sieve which retained any larvae. A gentle stream of air bubbles from a narrow bore glass tube gave gentle mixing and in the event of a failure of the water supply gave some aeration. The glass tubing ended 3 inches above the bottom of the bin so as to avoid disturbing the bottom deposit.

Table 12 Survival to post-metamorphosis in five large-scale larval rearing bins

Bin number	Initial number of larvae	Number of juvenile prawns produced		Percentage survival	Time in days before juvenile prawns removed from bins
1	14 500	5 415		37.3	20
2	9 100	4 325		47.5	18
3	9 700	4 540		46.8	21
4	7 000	3 140		39.3	21
5	10 000	1 080		10.8	18
Total	51 300	18 500	Mean	36.1	

Five replicate bins were set up with freshly-hatched larvae in the course of 1 week. The numbers of larvae added to each bin varied between 8 000 and 14 500. *Artemia salina* hatched in 48 hours from commercial dried eggs were supplied as food and maintained at a concentration of between 10 and 20 nauplii per ml. The level of *Artemia* was checked twice daily, at 0900 hours and at 1700 hours, and more nauplii were added as required.

The first larvae metamorphosed 15 days after the bins were set up, but the majority metamorphosed after 18–21 days; only 1–2 per cent of the survivors had not metamorphosed after this time. The newly-metamorphosed juveniles were removed from the bins by siphoning them into a sieve; they were then put into 50-litre tanks where the few remaining larvae were separated with a pipette. An average survival to post-metamorphosis of 36 per cent was achieved (Table 12) in spite of the low survival of 10.8 per cent in bin 5, for which there was no known cause.

LABORATORY WEANING OF NEWLY-METAMORPHOSED JUVENILES

Before the young juveniles were put into the outdoor tanks they were weaned in the laboratory from a live food diet on to prepared foods over a period of 2 weeks. Sixteen thousand of the 18 500 young juveniles were divided among three 280-litre fibre-glass tanks maintained at 20 ± 2°C, and fed with a mixture of *Artemia* nauplii, partially-grown *Artemia*, pieces of crab gonad and digestive gland, and chopped shrimp and mussel. After 2 weeks they had grown from an average live-weight of 5.50 mg to 15.50 mg and were taking prepared foods readily. The remaining 2 500 juveniles were transferred to a 140-litre fibreglass tank which was provided with a continuous flow of sea water at 10–12°C; they were fed with *Artemia* nauplii and grown *Artemia* but no prepared food. This procedure was adopted so that the survival of laboratory-weaned juveniles could be compared with juveniles weaned in outdoor tanks. By keeping these 2 500 juveniles in cold water in the laboratory for 2 weeks their further development was retarded, and they were therefore effectively unweaned when put into the outdoor tanks, having increased from 5.50 mg to only 5.91 mg average live-weight.

OUTDOOR REARING OF JUVENILES

The large-scale rearing of juveniles was continued outdoors through the summer months in twelve wooden tanks measuring 4 feet $\times$4 feet $\times$11 inches (approx. $1.2 \times 1.2 \times 0.3$ m), each of which was stocked with 500 juveniles. The tanks were constructed with 11 inch $\times \frac{3}{4}$ inch (approx. 28×2 cm) timber for the walls and $\frac{5}{8}$ inch (approx. 16 mm) marine plywood sheets for the bases. Each tank was painted with two coats of hard-heavy non-toxic brown paint. They were situated so that they were in direct sunlight for most of the day, although certain tanks, particularly numbers 7, 8, 9 and 10 (see Table 13) became shaded earlier in the evening than the others.

The depth of water was maintained at about 6 inches (15 cm), and aeration at the centre of each tank maintained the dissolved oxygen level. Every month the prawns were counted and a sample of 100 weighed. At the same time the tanks were scrubbed clean and refilled with clean sea water. Food, consisting of mussels on the shell, halves of crab, and crushed shrimp, was provided on plastic mesh trays, one to each tank; fresh food was added every 24 hours. The food rations were gradually increased to keep pace with the increasing appetites of the prawns. Initially three halves of mussel, two halves of crab and two crushed shrimps were added daily to each tank, and this was gradually increased over 2 months to ten halves of mussel, six halves of crab and three crushed shrimps.

The physical conditions in each of the tanks were varied so that their influence on the growth and survival of juveniles could be compared. A summary of the combinations of physical conditions tested is given in Table 13. Two of the tanks were provided with a continuous flow of sea water at approximately 2

litres per minute, and the other ten had static water which was half changed for clean sea water once a week. All but three of the tanks were protected from direct sunlight with translucent sheets of P.V.C., which were painted green; these covers reduced the light intensity at the water surface by 98.5 per cent. The other tanks were covered with $\frac{1}{4}$ inch (6 mm) plastic mesh which prevented the prawns from jumping out, but still left the tanks exposed to direct sunlight. The growth and survival of juveniles was therefore compared in direct and subdued sunlight, both in flowing and in static water (see Table 13, tanks 1, 2, 3 and 4). The influence of cover inside the tanks in the form of curved 5 inch $\times$3 inch (approx. 13 $\times$8 cm) sheets of black P.V.C., under which the prawns could hide in almost total darkness, was tested in direct and subdued sunlight (Table 13, tanks 5 and 6), and compared with tanks 3 and 4 which had no covers. Covers were also placed in the other tanks, i.e. numbers 7 to 12, where the influence of other factors was examined. Two of these tanks were provided with thermostatically-controlled 0.5 kW heaters which prevented the water temperature from falling below 18°C; from these the effect of low night temperatures, <7°C (see Table 15) during the early summer, could be estimated.

Other factors which did not concern the control of the physical environment were also tested. In tank 7 fresh food was added twice a day (except at weekends, when it was only added once), since it was thought that this might stimulate a higher feading rate and so improve growth; tank 8 was fed only once a day and was a control for tank 7. Tanks 10 and 12 were stocked with unweaned juveniles and were directly comparable with tanks 9 and 11, which were stocked with weaned animals. For the first 3 weeks after stocking both grown *Artemia* and *Artemia* nauplii were supplied to tanks 10 and 12 in addition to the normal prepared food rations; the animals were in this way weaned outdoors. The growth and survival of laboratory-weaned juveniles and juveniles weaned outdoors in heated and unheated static water was therefore compared in tanks 9, 10, 11 and 12. Tanks 5, 8 and 9 all had the same conditions (see Table 13), and as they were all stocked with laboratory-weaned juveniles they provided an estimate of the variation between replicates.

During the first 3 weeks after stocking (10 May–1 June 1967) high mortalities occured in most of the tanks, and particularly in the eight tanks with unheated static water. In tank 10, which was stocked with

Table 13 Summary of the different combinations of physical conditions tested in the large-scale outdoor rearing tanks. A cross indicates the condition in each tank

Tank number	Flowing water	Static water	Protection from sunlight	No protection from sunlight	Shelter in tank	No shelter in tank	Heaters in tank	No heaters in tank
1	X		X			X		X
2	X			X		X		X
3		X	X			X		X
4		X		X		X		X
5		X	X		X			X
6		X		X	X			X
7		X	X		X			X
8		X	X		X			X
9		X	X		X			X
10		X	X		X			X
11		X	X		X		X	
12		X	X		X		X	

500 unweaned juveniles, all of them died. Table 14 shows the survival and growth in each tank during the initial 3-week period; it is probable that the unusually cold weather during May was partially responsible for such heavy mortalities. Table 15 shows the maximum and minimum daily temperatures recorded

Table 14 Survival and growth of batches of 500 juvenile prawns in outdoor tanks during the first 3 weeks after stocking, from 10 May-1 June 1967

Tank number	Number of juvenile prawns after 3 weeks	Average live-weight (mg)	
		Initially	After 3 weeks
1	365	15.59	20.28
2	255	15.59	31.72
3	213	15.59	25.04
4	109	15.59	30.86
5	238	15.59	29.46
6	163	15.59	33.74
7	314	15.59	30.90
8	253	15.59	33.90
9	150	15.59	28.34
10	0	5.81	–
11	398	15.59	85.10
12	463	5.81	47.80

Table 15 Daily maximum and minimum temperatures (°C) recorded in tank 4 of the outdoor large-scale rearing experiment. The tank was not shielded from direct sunlight. The experiment was started on 10 May 1967

	Day	Min.	Max.		Day	Min.	Max.
May 11	1	13	14	Jun 3	24	14	20
12	2	12	13	4	25	11	19
13	3	11	13	5	26	14	24
14	4	6	8	6	27	11	18
15	5	6	9	7	28	10	22
16	6	8	10	8	29	10	20
17	7	8	18	9	30	12	22
18	8	10	17	10	31	11	26
19	9	8	14	11	32	13	26
20	10	10	12	12	33	10	25
21	11	8	13	1	34	14	24
22	12	9	14	14	35	14	26
23	13	11	15	15	36	14	26
24	14	11	20	16	37	16	27
25	15	11	18	17	38	16	26
26	16	11	14	18	39	16	22
27	17	12	14	19	40	16	18
28	18	10	21	20	41	12	17
29	19	12	16	21	42	14	20
30	20	10	26	22	43	12	20
31	21	12	20	23	44	15	18
Jun 1	22	10	22	24	45	14	19
2	23	14	19	25	46	14	20

Table 15—continued

		Day	Min.	Max.
Jun	26	47	14	21
	27	48	16	22
	28	49	15	19
	29	50	13	22
	30	51	14	20
Jul	1	52	15	23
	2	53	13	20
	3	54	14	21
	4	55	16	23
	5	56	17	20
	6	57	15	23
	7	58	14	19
	8	59	12	21
	9	60	16	27
	10	61	19	23
	11	62	17	25
	12	63	18	24
	13	64	19	22
	14	65	16	21
	15	66	17	22
	16	67	17	23
	17	68	17	23
	18	69	17	23
	19	70		
	20	71		
	21	72		
	22	73		
	23	74		
	24	75		
	25	76		
	26	77		16
	27	78	13	20
	28	79	14	18
	29	80	17	22
	30	81	17	20
	31	82	16	20
Aug	1	83	12	17
	2	84	13	18
	3	85	11	14
	4	86	10	19
	5	87	15	22
	6	88	15	23
	7	89	16	24
	8	90	16	22
	9	91	16	22
	10	92	15	18
	11	93	12	13
	12	94	11	16
	13	95	13	18
	14	96	12	18
	15	97	13	18
	16	98	13	18
	17	99	15	19
	18	100	15	17
	19	101	12	21
	20	102	13	23
	21	103	15	23

RECORD LOST

		Day	Min.	Max.
Aug	22	104	16	23
	23	105	17	20
	24	106	16	21
	25	107	17	20
	26	108	18	21
	27	109	16	20
	28	110	15	19
	29	111	13	16
	30	112	14	15
	31	113	11	16
Sep	1	114	14	18
	2	115	12	18
	3	116	12	16
	4	117	11	14
	5	118	10	15
	6	119	10	15
	7	120	9	17
	8	121	10	15
	9	122	12	16
	10	123	14	16
	11	124	15	17
	12	125	12	16
	13	126	11	17
	14	127	13	17
	15	128	13	16
	16	129	13	16
	17	130	13	17
	18	131	12	16
	19	132	10	14
	20	133	9	15
	21	134	10	14
	22	135	10	14
	23	136	10	13
	24	137	11	16
	25	138	13	16
	26	139	11	16
	27	140	12	15
	28	141	10	13
	29	142	11	13
	30	143	9	12
Oct	1	144	9	12
	2	145	7	10
	3	146	8	10
	4	147	9	14
	5	148	12	14
	6	149	12	13
	7	150	13	13
	8	151	12	14
	9	152	11	12
	10	153	7	9
	11	154	7	8
	12	155	7	7
	13	156	6	7
	14	157	7	8
	15	158	7	7
	16	159	7	8

throughout the summer in tank 4, which contained static water and was exposed to direct sunlight. Because it was exposed the temperature in this tank and also in the similar tank 6 fluctuated through a wider range than in any of the covered tanks. By comparison with the unheated static water tanks survival was improved in flowing water (tanks 1 and 2), and by the provision of heaters (tanks 11 and 12). Temperature records show that during the first 3 weeks the temperature of the flowing water never fell below 10°C, whilst the heated tanks did not fall below 18°C. It is likely that either the low temperatures or the large temperature fluctuations which occurred in the unheated static water tanks were the primary cause of the initially high mortalities. However, since later juveniles survived well in these tanks during the rest of the summer, when even greater temperature fluctuations occurred (Table 15), it is considered unlikely that temperature fluctuations alone were a major cause of mortality.

Table 16 Survival and growth of prawns in outdoor tanks, 1-6, 9 and 10, restocked 1 June 1967 (Day 1 = 1 June)

Tank number	Number of prawns surviving on day						Average live-weight (mg) of prawns on day					
	0	25	53	83	110	138	0	25	53	83	110	138
1	500	460	436	416	365	288	127.2	260.3	518.6	830.6	1 083	1 240
2	500	454	449	434	367	269	127.2	257.9	602.8	806.0	1 071	1 291
3	500	482	461	401	360	312	127.2	292.6	592.6	807.4	1 039	1 166
4	500	454	435	403	388	369	127.2	249.9	471.0	750.4	1 033	1 230
5	500	493	450	445	249*	230	127.2	255.1	480.2	759.8	981*	1 191
6	500	395	232*	207	201	187	127.2	232.1	561.0*	834.8	1 121	1 335
9	500	483	480	441	417	368	85.5	229.3	491.6	670.8	956	1 020
10	500	441	436	417	401	374	85.5	234.9	495.6	696.8	1 010	1 104

*Denotes accidental mortalities due to air failure.

Table 17 Survival and growth of prawns in outdoor tanks 7, 8, 11 and 12, first stocked 10 May 1967 and not restocked 1 June 1967 (Day 1 = 10 May)

Tank number	Number of prawns surviving on day							Average live-weight (mg) of prawns on day						
	0	21	46	74	104	131	159	0	21	46	74	104	131	159
7	500	314	297	292	283	282	249	15.59	30.90	158.7	474.6	839.8	1 061	1 287
8	500	253	227	223	216	216	209	15.59	33.90	178.1	545.8	978.8	1 204	1 439
11	500	398	374	362	331	287	276	15.59	85.10	262.5	595.2	832.0	1 103	1 375
12	500	463	460	418	344	–*	–	5.81	47.80	272.2	494.0	746.2	–*	–

*Denotes accidental mortalities due to air failure.

Since survivals were so low during the initial 3 weeks, eight of the tanks (numbers 1 to 6, 9 and 10) were restocked on 1 June with 500 more juveniles which had been kept in the laboratory since metamorphosis. The conditions in tanks 1 to 6 were not altered but those in tanks 9 and 10 were changed and became replicates of tanks 3 and 5 respectively. Since survivals and growth had been quite good in the heated tanks 11 and 12 they were not restocked, neither were tanks 7 and 8, so that a direct comparison was made between the growth of young juveniles in heated and unheated static water.

After restocking mortality was very low. There were, however, three accidents (indicated in Tables 16 and 17) when the air supply to particular tanks failed and high mortalities resulted. The survival and growth up to 16 October, 138 days after restocking, are shown in Table 16. Table 17 shows the survival and growth in tanks 7, 8, 11 and 12 which were not restocked at the beginning of June.

The results show that there was no particular advantage conferred by any one set of conditions. Neither growth nor survival was enhanced by a continuous flow of water, and towards the end of the experiment several instances of *white tail* disease (see page 2) were recorded in both flowing water tanks, while there were very few such cases in the static water tanks. This accounts for the comparatively heavy mortalities seen in tanks 1 and 2 between days 110 and 138 after restocking (see Table 16). The cause of *white tail* is still not known, but all the cases recorded in tanks 1 and 2 were characterized by a missing abdominal appendage and erosion of the cuticle at the site of the wound.

Exposure to direct sunlight had no adverse effects. However, the water in the exposed static water tanks was characterized by rich blooms of unicellular algae, mostly *Phaeodactylum* sp., and an unidentified non-motile unicellular green species. The quantity of light reaching the bottom of these tanks was therefore greatly reduced, especially towards the end of a week before the water was half changed. The presence of shelter for the prawns inside the tanks had no marked influence, neither did the provision of fresh food twice a day. The complete failure of the unweaned juveniles to survive the initial low temperatures suggests that a 2-week period of laboratory weaning, with the protection from the low temperatures likely to occur in the early summer, is advantageous. This was supported by the success of the unweaned juveniles in tank 12 in which the temperature conditions were similar to those of the laboratory.

The growth of prawns in tanks 7 and 8, which were not restocked at the beginning of June, was unexpectedly as good as the growth in the heated tanks 11 and 12, and slightly better than the average growth recorded for the restocked tanks 1–6, 9 and 10. The explanation is uncertain and is probably a combination of several factors. It is possible that the low temperatures killed most of the weaker slower-growing prawns, while the strong faster-growing ones survived, but this is not supported by the size distribution at the end of the experiment. Total length measurements made on the prawns from tanks 8 and 10 (see Figure 8) show that there was an equally wide distribution of sizes in both tanks, between 41 and 69 mm (mean 55.58 mm) in tank 8, and between 40 and 65 mm (mean 50.53 mm) in tank 10. Both patterns of distribution were similar and this suggests that slow-growing prawns were not selectively killed during the first 3 weeks in tanks 7 and 8. It is considered likely, therefore, that the lower population densities resulting from the early mortalities in tanks 7 and 8 in some way favourably influenced growth.

Population density, however, may not be the only factor involved, since a comparison of the sex ratios in tanks 8 and 10 revealed that there was a higher proportion of females in tank 8 than in tank 10:

Observations	Tank number	
	8	10
Percentage of females	24.88	9.70
Percentage of males	75.12	90.30
Mean length of females (mm)	59.8	56.5
Mean length of males (mm)	53.5	49.7

A χ^2test showed that the difference between the ratios was significant ($\chi^2 = 23.386$; $P < 0.001$). However, the mean length of each sex in tank 8 was greater than that in tank 10, these differences being highly significant (standard deviation = 3.47; $P < 0.001$ for the females, and standard deviation = 9.69; $P < 0.001$ for the males). Therefore the different sex ratios only partly explain the unexpectedly good growth in tank 8, and it seems probable that the differences in population density which occurred as a result of the high initial mortalities in tanks 7 and 8 may have played an important part. These sex ratios are abnormal, compared with wild populations, in which the ratio of the sexes in prawns above 30 mm (below which they cannot be easily sexed) is approximately 1:1. For example, a small sample of juveniles captured with a hand net during October in Anglesey gave a ratio very close to 1:1, and in a sample of 1 138 adults captured offshore in pots at Weymouth in November 1966 the ratio was 605 males: 503 females. Forster (1951) reports that during the summer months in Plymouth, when the whole of the prawn population under observation was close inshore, there was a slight majority in favour of females. Cole (1958) also found a slight majority of females in samples from North Wales.

The reasons for these unequal sex ratios in culture conditions are not known, but it is possible that a high proportion of wild larvae are potential males, and that in the natural environment males have a higher rate of mortality than females. Under culture conditions larval mortality is reduced, with the result of a preponderance of males. Lloyd and Yonge (1947) showed that male *Crangon vulgaris* were more susceptible to low temperatures and salinities (winter conditions) than females. If this explanation is correct, it has

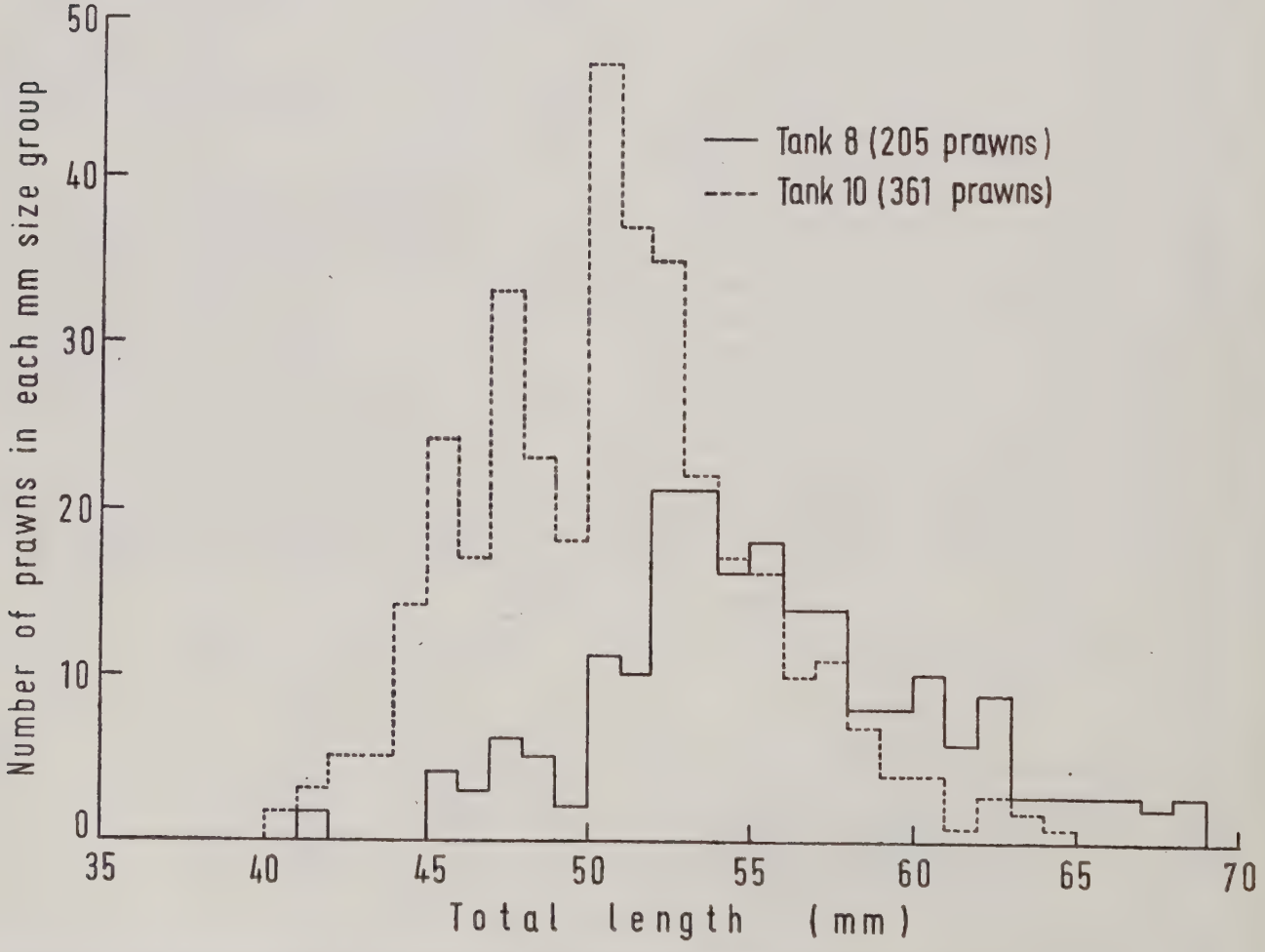

Figure 8 Size distributions of prawns from two outdoor large-scale rearing experiments.

important implications if the commercial culture of *P. serratus* is considered, since it is only the females which commonly reach an optimum commercial size of between 6 and 8 g. Alternatively, these abnormal ratios may be explained if at some stage during early development sexual differentiation is influenced by environmental factors and that certain culture conditions cause a bias towards differentiation as males. Kinne (1953) showed that the sex ratio of broods of *Gammarus duebeni* was influenced by the temperature at which the egg-carrying females were kept, and also by the temperature at which the males were kept prior to copulation. If this applies to prawns it may have even further implications for commercial culture, since by adjustment of the environmental conditions at the right time during early development, it might be possible to produce more females than males.

A comparison of the growth of juveniles in the restocked tanks (1–6, 9 and 10) with the growth of juveniles in the laboratory at 18–22°C shows that the laboratory populations grew better. It took 138 days for the outdoor prawns to grow from 0.117 to 1.197 g average live-weight, compared with approximately 90 days for laboratory prawns to show the same increase. Nevertheless, the results of this first attempt at outdoor large-scale rearing were encouraging and demonstrate the feasibility of applying experimental rearing techniques on a larger scale.

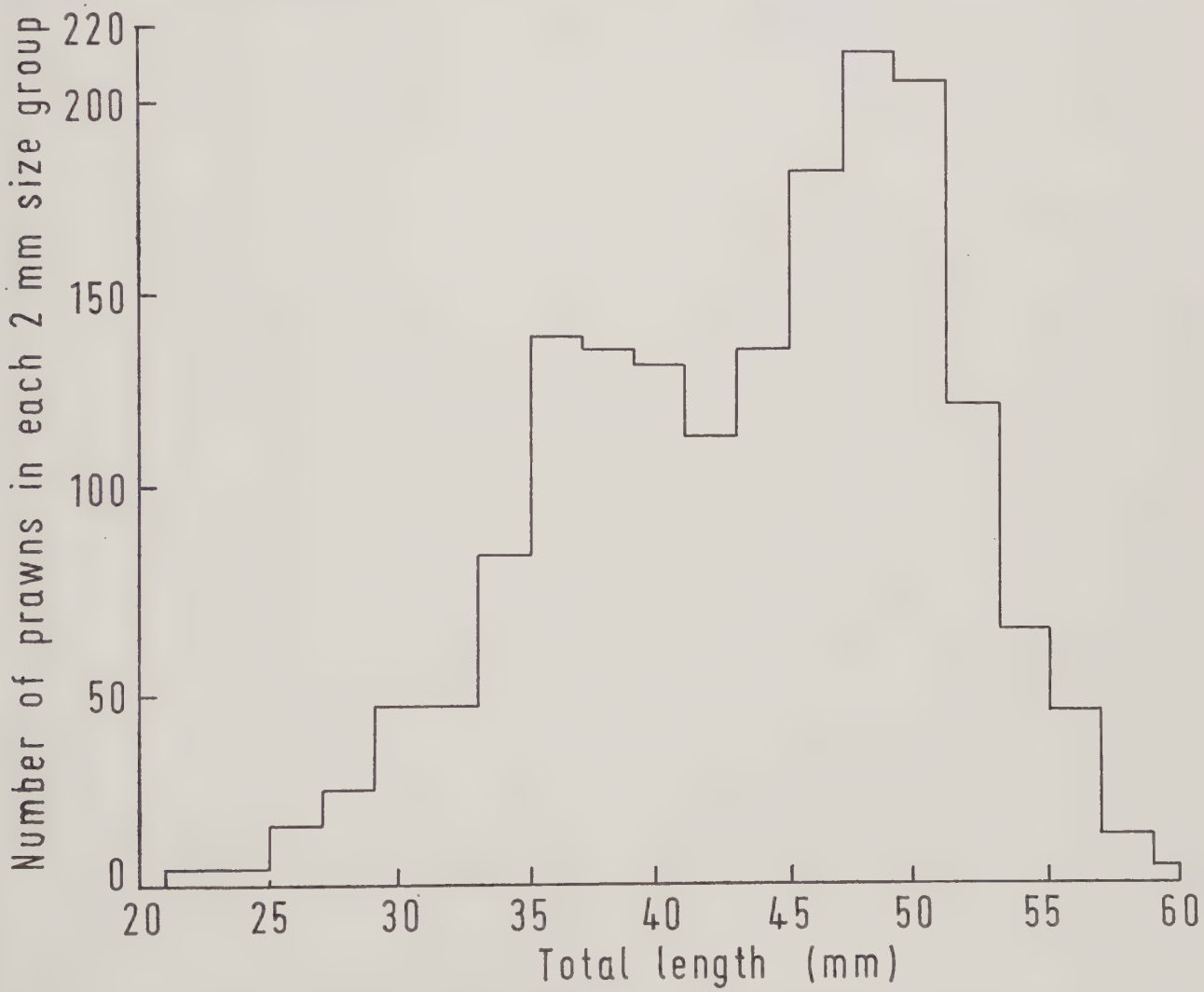

Figure 9 Size distribution of 1 740 juvenile prawns taken from an outdoor concrete tank in which they had been reared for 127 days.

This was further demonstrated when between 11 and 25 July 1967, 7 000 early juveniles which had been weaned in the laboratory were put outdoors into a concrete tank measuring 10 feet $\times$ 5 feet $\times 2\frac{1}{2}$ feet (approx. $3.0 \times 1.5 \times 0.8$ m). The tank contained static sea water which was half changed every 2 weeks. Throughout late July and August the water temperature in the tank varied between 17 and 20°C and gradually fell to 14°C during September. Crushed shrimp and halves of mussel and crab were provided as food on plastic mesh trays.

The tank was drained, the prawns counted, and a sample of 200 measured on 30 September, 74 days after the first juveniles were added; 5 000 (71.4 per cent) had survived and grown to an average total length of 38 mm (0.45 g). The tank was refilled and the prawns kept for a further 53 days until 22 November. At this time the water temperature had dropped to 1.5°C following a spell of particularly cold weather. This is well below the lower lethal temperature of about 4°C, and it is probable that mass mortalities would have occurred had the prawns been left outdoors much longer. As it was, many corpses were found, together with 2 840 survivors, when the tank was drained. A sample of 1 740 prawns were measured and sexed, and the average total length was found to be 43 mm (0.64 g). The numbers of each sex were 1 300 males, 348 females, and 92 below 30 mm which were not sexed. A very wide variety of sizes (21 to 60 mm) was found in these prawns (see Figure 9), which had not occurred among other laboratory-reared animals or among those prawns reared in outdoor wooden tanks (see above).

Conclusions

Although there is still much work that needs to be done, particularly concerning the problems of nutrition, growth at low temperatures (6–18°C), and the growth of mature prawns, the results of Reeve's work and of the experiments described in this paper suggest that the development of the rearing technique to a commercial scale would be possible.

The high survivals (average 36.1 per cent) obtained in the large-scale larval rearing experiment were particularly encouraging. Reeve (1969) thought that survivals between 35 and 45 per cent (the average survival in small-scale experiments) of larvae in mass culture would not be realized initially, partly because of the difficulty of dispersing larvae, which tend to aggregate in large numbers, and partly because there was likely to be considerable variation between the growth of different broods. Both these factors would tend to increase cannibalism. The results of the experiments described above, however, show that these problems may not be serious. The almost simultaneous metamorphosis of the larvae in each rearing bin suggests that brood variation may be only slight, and the tendency of larvae to aggregate can be reduced by using black-walled rearing vessels. The high survivals of juveniles in the outdoor experiments (average 52.5 per cent, which was achieved in spite of the three accidents when the air supply failed in three of the tanks) shows that the problems of cannibalism can be reduced to a tolerably low level, and the maturation and successful spawning of one laboratory-reared female suggests that prawns will fully adapt to culture conditions. Their suitability for culture was further shown by their tolerance of a wide range of physical conditions and the good survivals recorded in static turbid water.

The economic feasibility of mass culturing *P. serratus* remains in doubt, however, since there are certain aspects of the biology of this species which at present appear to be inherent handicaps. Firstly, prawns will not survive for more than a few days at temperatures below 4°C, and therefore if large numbers of prawns are to be overwintered in outdoor tanks supplementary heating would be required, thereby increasing costs. Secondly, it is the females only which reach an optimum commercial size of between 6 and 8 g. Males are rarely found larger than 5.0 g and therefore not all the cultured animals would fetch maximum prices. This would be especially important if the sex ratios favouring males found in the large-scale experiments (see above) occur regularly and cannot be reversed. Thirdly, laboratory observations have shown that male prawns usually mature at about 2.0 g and females between 3.0 and 3.5 g live-weight, which is well below the optimum commercial size of 6 to 8 g. After maturation, a considerable part of the food will be used in the development of the gonads which, under good conditions, may ripen three times in one year. Following maturation, therefore, the growth rate will almost certainly slow down, although the decline may not be quite as marked as was shown in Figure 2 for an all-male population. Furthermore, the growth efficiency (increase in live-weight/weight of food eaten) will be less, since much of the food eaten will be used in the development of the gonads. This decline in growth and the associated reduction in growth efficiency would inevitably increase rearing costs. A fourth and final drawback is that the overall growth rate itself is slow. At the time of writing a laboratory-reared population which has been kept at 20 ± 2°C for 9 months since metamorphosis has reached an average live-weight of 2.6 g. When the sexes were weighed separately the males averaged 2.0 g and the females 3.2 g live-weight. Under laboratory conditions it would probably take between 15 and 18 months for females to reach an optimum commercial size; in unheated outdoor tanks it would take considerably longer. With further development and improvement of rearing techniques the growth rate may be improved, but it is most unlikely that prawns could ever be grown to an optimum commercial size in under 12 months, even if suitable temperatures were maintained.

For these reasons it may prove very difficult to make the culture of *P. serratus* a commercial success. However, the possibility cannot be ruled out, since it may be practicable to reduce costs by employing the large quantities of heated sea water discharged as cooling effluent from certain electricity generating stations. It may also be possible to reduce costs even further by using very cheap sources of food such as offal, the by-catch from commercial fishing vessels, or even the food meals and concentrates used in the feeding of cattle and pigs, if such foods could be suitably prepared for prawns.

Because of the limitations of *P. serratus* as an animal for commercial culture, it would be worth studying

the feasibility of culturing other species of Decapod Crustacea which have more favourable characteristics. Two species have already been cultured successfully, *Penaeus japonicus* by Hudinaga (1942), Hudinaga and Miyamura (1962) and Hudinaga and Kittaka (1967), and *Macrobrachium rosenbergii* by Ling and Merican (1962) and Ling (1967*a*, *b*). Both these animals have excellent growth characteristics. *M. rosenbergii* will reach 100 g in 9 months, provided that the temperature is maintained at 26–28°C (Ling 1967a). According to Hudinaga and Miyamura (1962) *P. japonicus* grows to 20–25 g in a year under intensive cultivation, and even then the growth rate is slow by comparison with individuals in the natural environment. Although the optimum temperature range for *P. japonicus* is 25–28°C the growth to 20–25 g in a year was achieved in outdoor ponds, where the temperature reached 30°C in the summer and dropped as low as 10°C during the winter when growth ceased.

In addition to the two species mentioned above, there are three American Penaeidae, whose culture has received attention in the United States; they are *P. aztecus*, *P. duorarum* and *P. setiferus*. These too have good growth characteristics; for example, *P. setiferus* juveniles were grown in salt-water ponds from 1 to 30 g in one year (Johnson and Fielding 1956). However, like *P. japonicus* and *M. rosenbergii*, these American Penaeids thrive in warm water. Zein-Eldin and Griffith (1966) have shown in laboratory experiments that *P. aztecus* grows best within the temperature range 27.5–32.5°C, although survival was best between 20 and 25°C. Another penaeid prawn, *P. monodon*, the fry of which are captured and cultured in ponds in the Philippines (Delmendo and Rabanal 1956, and Caces-Borja and Rasalan 1967), will grow to 100 g in one year, but again high temperatures, between 25 and 29°C, are required.

For the species discussed above, the requirement of water at 25–30°C in order to achieve their excellent growth rates would create considerable economic difficulties if their culture were to be undertaken in the United Kingdom. But they should not be dismissed as candidates for commercial culture in this country on these grounds. The enormous potential of such species, which might yield three or four harvests per year if they were sold as juveniles of 8 to 12 g, would almost certainly compensate for the extra expense of heating water. In suitably insulated tanks, under cover, where the water is continually recirculated through filters, the cost of maintaining a water temperature between 25 and 30°C could be brought down to reasonable proportions, and it is quite possible that the culture of these warm-water species would be economically viable.

Ideally, for culture in this country a prawn is required which exhibits growth characteristics similar to those of the warm-water species discussed above, but which normally inhabits temperate, or even polar, waters. Williamson (1967) and Dobkin (1967) suggest that the possession of an abbreviated larval life-history should be another criterion in the choice of prawn for culture. Such a life-history would greatly reduce larval mortalities and shorten the time that live food need be supplied to the young animals. Williamson suggests that *Sclerocrangon boreas*, which has no pelagic larval stage, may have considerable potential for culture purposes. It is a large prawn, reaching 12 cm in length (*P. serratus* rarely reaches 12 cm), and is widely distributed in the colder waters of both the North Atlantic and the North Pacific oceans. There is no information on its growth rate. Prawns such as *S. boreas* which have an abbreviated larval life-history also have a low fecundity. This would present serious problems is the event of commercial culture, since large numbers of egg-carrying females would be needed to provide sufficient juveniles. The costs of obtaining and holding such stocks may well offset any saving made as a result of reduced larval requirements. It might be possible, if the reared animals could be successfully spawned under culture conditions, to use such animals as breeding stock, and to harvest them only after they have spawned for the first time. Although this would eliminate the need for holding a large breeding stock, it would introduce extra complications into a rearing procedure which would be undesirable.

There are some other temperate-water species which also appear to have certain potential for culture. Some of the northern water pandalids may be suitable; for instance *Pandalus platyceros* grows to 6.5 g in 1 year and reaches 35 g in $3\frac{1}{2}$ years in the wild at temperatures between 7 and 10°C (Butler 1964). A possible disadvantage is that pandalids generally inhabit deep water and may present special problems in terms of highly specific requirements. There are also two South American penaeids, *Artemesia longinaris* and *Hymenopenaeus mulleri*, which may repay investigation. They inhabit waters of between 9 and 22°C and the latter reaches a size of 40 g (Angelescu and Boschi 1959), although the time taken to reach this size is not known.

There are no doubt many other lesser-known species, both in the northern and southern hemispheres, which may be suitable for culture in this country. It is suggested by Williamson (1967) that the consideration of species for culture should not be limited to those animals which are abundant in nature, and this is fully endorsed by the author. However, the great potential of some of the species mentioned above would seem to justify immediate investigation, and it is hoped that the rearing techniques which have been established for *P. serratus* will be helpful in such work.

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References

ANGELESCU, V. and BOSCHI, E. E., 1959. Estudio Biologico Pesquero del Langostino de Mar Del Plata en conexión con la Operaracion Nivel Medio. *Publnes Serv. Hydrogr. nav. Repub. Argent.*, No. H.1017.

BEVERTON, R. J. H. and HOLT, S. J., 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, **140** (1), 67–83.

BUTLER, T. H., 1964. Growth, reproduction and distribution of pandalid shrimps in British Columbia. *J. Fish. Res. Bd Can.*, **21,** 1403–52.

CACES-BORJA, P. and RASALAN, S. B., 1967. A review of the culture of sugpo *Penaeus monodon* Fabricius in the Philippines. *FAO Wld Sci. Conf. Biol. Cult. Shrimps and Prawns, Mexico City, 12–24 June, 1967*, Preprint FR: BCSP/67/R/4, 13 pp. (mimeo).

COLE, H. A., 1958. Notes on the biology of the common prawn, *Palaemon serratus* (Pennant). *Fishery Invest., Lond.*, Ser. 2, **22** (5), 22 pp.

DELMENDO, M. N. and RABANAL, H. R., 1956. Cultivation of 'Sugpo' (Jumbo Tiger Shrimp) *Penaeus monodon* Fabricius in the Philippines. *Proc. Indo-Pacif. Fish. Coun.*, **6** (3), 424–31.

DOBKIN, S., 1967. Abbreviated larval development in Caridean shrimps and its significance in the artificial culture of these animals. (Abstract.) *FAO Wld Sci. Conf. Biol. Cult. Shrimps and Prawns, Mexico City, 12–24 June, 1967*, Preprint FR: BCSP/67/E/53, 2 pp. (mimeo).

FORSTER, G. R., 1951. The biology of the common prawn *Leander serratus* Pennant. *J. mar. biol. Ass. U.K.*, **30,** 333–60.

HIATT, R. W., 1948. The biology of the line shore crab *Pachygrapsus crassipes* Randall. *Pacif. Sci.* **2,** 135–215.

HUDINAGA, M., 1942. Reproduction, development and rearing of *Penaeus japonicus*. *Jap. J. Zool.*, **10,** 305–93.

HUDINAGA, M. and KITTAKA, J., 1967. The large-scale production of the young Kuruma prawn *Penaeus japonicus* Bate. *Inf. Bull. Planktol. Japan, Matsue Commem. Vols*, 35–46.

HUDINAGA, M. and MIYAMURA, M., 1962. The breeding of the 'Kuruma' prawn *Penaeus japonicus* Bate. *J. oceanogr. Soc. Japan, 20th Anniv. Vol.*, 695–706.

JOHNSON, M. C. and FIELDING, J. R., 1956. Propagation of the white shrimp *Penaeus setiferus* (*Linn.*) in captivity. *Tulane Stud. Zool.*, **4,** 173–90.

KINNE, O., 1953. Zur Biologie und Physiologie von *Gammarus duebeni* Lillj., VII. Über die Temperaturabhängigkeit der Geschlechtsbestimmung. *Biol. Zbl.*, **72,** 260–70.

KURATA, H., 1962. Studies on the age and growth of Crustacea. *Bull. Hokkaido reg. Fish. Res. Lab.*, No. 24, 1–115.

LING, S. W., 1967a. Methods of rearing and culturing *Macrobrachium rosenbergii* (de Man). *FAO Wld Sci. Conf. Biol. Shrimps and Prawns, Mexico City, 12–24 June, 1967*, Preprint FR: BCSP/67/E/31, 11 pp. (mimeo).

LING, S. W., 1967b. The general biology and development of *Macrobrachium rosenbergii* (de Man). *FAO Wld Sci. Conf. Biol. Shrimps and Prawns, Mexico City, 12–24 June, 1967*, Preprint FR: BCSP/67/E/30, 18 pp. (mimeo).

LING, S. W. and MERICAN, A. B. O., 1962. Notes on the life and habits of the adults and larval stages of *Macrobrachium rosenbergii* (de Man). *Proc. Indo-Pacif. Fish. Coun.*, **9** (2), 55–61.

LLOYD, A. J. and YONGE, C. M., 1947. The biology of *Crangon vulgaris* L. in the Bristol Channel and Severn Estuary. *J. mar. biol. Ass. U.K.*, **26,** 626–61.

PANNIKAR, N. K., 1940. Osmotic properties of the common prawn. *Nature, Lond.*, **145,** p. 108.

PLANKEMANN, H., 1935. Contribution to the physiology of moulting in prawns. *Schr. naturw. Ver. Schlesw.-Holst.*, **21,** 195–216. (English translation, UKAEA, Chapelcross, No. CC/17.)

REEVE, M. R., 1969. The laboratory culture of the prawn *Palaemon serratus. Fishery Invest., Lond.*, Ser. 2, **26** (1) 38 pp.

WALNE, P. R., 1966. Experiments in the large-scale culture of the larvae of *Ostrea edulis* L. *Fishery Invest., Lond.*, Ser. 2, **25** (4), 53 pp.

WILLIAMSON, D. I., 1967. The type of development of prawns as a factor determining suitability for farming. *FAO Wld Sci. Conf. Biol. Shrimps and Prawns, Mexico City, 12–24 June, 1967*, Preprint, FR: BCSP/67/R/1, 6 pp. (mimeo).

ZEIN-ELDIN, Z. P. and GRIFFITH, G. W., 1966. The effect of temperature upon the growth of laboratory-held post- larval *Penaeus aztecus. Biol. Bull. mar. biol. Lab., Woods Hole*, **131,** 186–96.

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